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Patterns of Reef Fish Larval Supply to Petroleum Platforms in the Northern Gulf of Mexico.

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PATTERNS OF REEF-FISH LARVAL SUPPLY TO PETROLEUM PLATFORMS IN THE NORTHERN GULF OF MEXICO

A Dissertation

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by
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ABSTRACT

Surveys of ichthyoplankton assemblages were conducted from four oil and gas platforms located in the northern Gulf of Mexico from November 1994 through July 1997. Diurnal collections, supplemented with light trap collections from the surface and -20 m depth, were taken quarterly during 1994 and 1995. Quarterly ichthyoplankton sampling at dawn and dusk only during 1996 and 1997 were supplemented with surface "lighted plankton net" collections. Of the 36,676 individuals collected, epipelagic (neretic and oceanic Clupeiformes, neretic Carangidae and Lutjanidae, as well as oceanic Scombridae) and mesopelagic (Myctophidae and Gonostomatidae) families comprised the majority of the ichthyoplankton. Reef-dependent (e.g., Pomacentridae, Labridae, and Acanthuridae) families that dominated the adult fish communities at the platforms were either absent or very rare from both ichthyoplankton and light trap collections.

Large-scale water mass movements, which primarily determine the transport of planktonic organisms as well as the linkage between potential source (natural reefs, hard bottom banks, and other platform structures) and sinks (platform artificial reef sites) were investigated with blended TOPEX / POSEIDON and ERS-2 radar altimetry. Serranid larvae collected from the plankton were aged by use of sagittal otoliths in order to estimate their transit time from natal source areas. Transit time in the plankton averaged 14.5 days. Seasonal transport envelopes showed that recruitment to mid-shelf and shelf-break platforms were influenced primarily by

mesoscale warm-core and cold-core eddies. Within these seasonal envelopes, the numbers of artificial reef platforms potentially serving as source locations for recruitment greatly outnumbered the natural reef sites.

Scuba diver and remotely operated vehicle surveys of juvenile and adult stage reef-dependent species were also conducted on the mid-shelf and shelf-break platforms. These were compared to underwater video footage of natural reef sites (National Marine Fisheries Service, SEAMAP fish trap/video gear) in order to establish correspondence between the taxa supplied to the platforms and the surrounding hard-bottom communities. Bray-Curtis similarity cluster analysis and multidimensional scaling of adult and juvenile reef-dependent fish communities showed that platform habitats had a biological character more like natural reef sites found in the eastern Gulf of Mexico, where little recruitment was shown to originate.

INTRODUCTION

Reef fishes constitute a major component of tropical and subtropical ichthyofaunal communities, and often support important commercial, recreational, and artesinal fisheries worldwide. Their life history strategies typically follow a bipartite cycle (Leis 1991b). Adults, who are often found closely associated with benthic structure, produce pelagic offspring that can be dispersed great distances from natal reefs (Ehrlich 1975; Richards and Lindeman 1987; Schultz and Cowen 1994, Thorrold et al. 1994a). Whether eggs and sperm are broadcast directly into the water column, or brooded eggs are afforded some protection until hatching (Barlow 1981), propagules ultimately enter a planktonic phase lasting from weeks to months (Sale 1980; Thresher 1984). Of the thousands of species native to coral reefs, only a handful lack this pelagic early life stage.

Spawning adults cannot anticipate the conditions that their offspring will encounter, and consequently their reproduction is characterized by high risk and near total mortality (Johannes 1978; Bailey and Houde 1989; Roberts 1991; Doherty and Fowler 1994). To compensate for the high mortality in the plankton, many reef fishes produce large numbers of small offspring, and may spawn numerous times throughout the year (Breder and Rosen 1966; Rothschild 1986). Local population sizes, as well as the species composition of adult assemblages, can ultimately be determined by pelagic-stage processes (Doherty 1983, 1987a; Richards and Lindeman 1987; Doherty and Williams 1988a; Underwood and Fairweather 1989; Meekan et al. 1993).

Because coral reefs are spatially disjunct and reef fish are normally sedentary as adults, the dominant recruitment to local reef populations comes from the settlement of planktonic larvae (McFarland and Ogden 1985). These "open" populations (marine populations that are replenished by pelagic propagules) typically show large interannual, spatial and temporal fluctuations in abundance due to recruitment-limitations (Lobel and Robinson 1983; Eckert 1984; Schoreder 1985; Doherty and Williams 1988b; Milicich et al. 1992; Doherty and Fowler 1994b; Kingsford and Finn 1997). Variations in the replenishment (i.e., supply-side) of larvae have been identified as one of the determining factors in the population sizes of reef fishes. Local shortages of competent larvae can keep reef fish populations below levels at which food or space limitations which would ultimately determine the carrying capacity of a benthic habitat (Williams 1980; Doherty 1982; Victor 1983; Warner and Hughes 1989). Similarly, supply-side recruitment processes have also been shown to regulate the structure of many marine invertebrate communities (Mileikovsky 1971; Caffey 1985; Roughgarden et al. 1985; Sutherland 1987; Underwood and Fairweather 1989; Garvine et al. 1997).

Transport mechanisms influencing the early life histories of reef fishes also tend to increase the variability of recruitment and ultimately adult abundance (Cowen 1985; Able et al. 1995). For fishes with an extended larval duration, many highly interrelated dynamic oceanographic and meteorological processes operating at micro- through macro-scales can influence planktonic survivorship. Dispersal (or retention) of larvae from natal reefs can be influenced by geostrophic and wind-induced current patterns, topographically-steered flows, Langmuir circulation cell convergence, upwelling, wind-

induced surface layer mixing, temperature, salinity, nutrient discontinuity zones, frontal zones of gyres, eddies, coastal plumes, tidal forces and boundary layer dynamics (Leis and Miller 1976; Hannan 1984; Norcross and Shaw 1984; Yoder 1984; Young et al. 1986; Cowen et al. 1993; Schultz and Cowen 1994). Acting in concert with these physical factors are additional biological processes aiding in the dispersal or retention of larval reef fishes; such processes include behavioral and sensory-mediated control of vertical movement, swimming, and buoyancy (Boehlert et al. 1992; Lamkin 1997). While a clear understanding of the numerous density-independent physical processes operating along transport routes is necessary to explain the presence of certain species assemblages, hydrographic parameters alone have repeatedly failed to resolve much of the inherent variability encountered in larval dispersal, distribution, and subsequent recruitment (Cowen et al. 1993).

Piscivory of post-settlement juveniles on individual reefs is another source of mortality that can ultimately shape adult abundance patterns (Smith 1978; Doherty and Sale 1985; Jones 1991; Carr and Hixon 1995). Influxes of new individuals to reef populations and their interaction with resident species can lead to resource partitioning and competition, additionally controlling local abundance patterns (Anderson et al. 1981; Sale 1982; Doherty 1983; Sale and Ferrell 1988; Holm 1990; Hixon 1991; Kaufman et al. 1992; Sale et al. 1994). The major processes structuring reef fish communities; e.g., recruitment limitation, competition, and predation, should not be viewed as mutually exclusive hypotheses, but more properly, a continuum of overlapping alternatives (Hixon 1991; Hixon and Beets 1993).

Open populations rely on water mass circulation for the distribution of their larvae (Caswell 1978), and the dominant large-scale transport feature in the Gulf of Mexico (Gulf) is the Loop Current. Cyclonic eddies shed off the Loop Current, along with their closely associated anti-cyclonic features (Elliot 1982) impact the outer continental shelf region and have the potential to modify the dispersal patterns of pelagic reef fish larvae on the Texas-Louisiana, Mississippi-Alabama, and the West Florida shelves (Li et al. 1997).

Since the 1940's, approximately 4,400 offshore oil and gas production platforms have been located in the U.S. Federal waters of the northern Gulf. Although these structures represent only a tiny fraction of the total available hard-bottom area (approximately 0.4 % of the total on the northern Gulf continental shelf, see Gallaway 1998), most platforms are located in areas of limited natural reef sites. The degree to which platform reef fish populations are interconnected depends upon the dispersal capabilities of the species involved, the dominant hydrographic regime, the physical distance separating platform habitats, and the availability of suitable habitats for colonization. Because platforms provide hard-bottom living space traversing the entire water column from the surface to the ocean floor, each can be effectively viewed as an artificial reef island, relying on other locations for their replenishment supply of reef fish recruits.

CHAPTER 1: REEF FISH ICHTHYOPLANKTON SUPPLY TO OIL AND GAS "ARTIFICIAL REEF" PLATFORMS

Introduction

Many fish species, particularly reef fishes, tend to congregate in areas of pronounced topographical changes of the sea bottom (Mottet 1986). The natural reefs and hard-bottom rock outcroppings scattered throughout the otherwise low-relief continental shelf of the Gulf of Mexico (Gulf) provide such topographical highs (Parker and Curray 1956; Cashman 1973). Parker et al. (1983) estimated approximately 2,780 km^2 of available natural reef habitat exists on the continental shelf within the central and western Gulf. The reef fish biota associated with these habitats represents a mix of western Atlantic temperate and insular tropical species, becoming predominantly tropical in the more offshore areas (Dennis and Bright 1988).

Increased fish abundance associated with natural reefs and "live bottom" areas have been previously correlated with structural complexity (Luckhurst and Luckhurst 1978), prey accumulation (Kilma and Wickham 1973; Murray et al. 1987), and habitat utilization (Roundtree 1989; Potts and Hulbert 1994). Factors determining the maintenance of these hard-bottom communities include winter temperature minimums (Rezak et al. 1985), riverine influences on salinity, turbidity, and sedimentation (Bright and Pequegnat 1974), depth and thickness of the nepheloid layer (Shideler 1981), and depth and geological characteristics of the substrate (Bright and Rezak 1978).

Though reef fishes are commonly reported from the northern Gulf (Caldwell 1959; Robins 1971, Hastings 1972; Cashman 1973; Bright and Pequegnat 1976; Hastings et al. 1976; Sonnier et al. 1976; Bull and Kendall 1994), the relatively rapid deployment of this large network of artificial reefs (4,000+ platforms) has undoubtedly increased the established range of many tropical species. These platforms create dynamic artificial reef ecosystems by providing hard substrate throughout the entire water column, which is quickly colonized by sessile organisms such as algae, barnacles, and hydrozoans (Shinn 1974; Dokken et al. 1993). These in turn create suitable habitat for secondary colonization by polycheates, mollusks, crustaceans, echinoderms, and tunicates, eventually forming a complex biofouling community. The biofouling mat constitutes the base of the platform community trophic web, providing prey and shelter for nekton fish species in an open ocean environment (Gallaway and Lewbel 1982). It is quite likely that these platforms, which provide a greatly exaggerated topographical change in the sea bottom, influence fisheries resources (Bull and Kendall 1994).

Larval settlement onto artificial reefs, as well as secondary colonization by both older juveniles and adults, is typically rapid (Bohnsack et al. 1994; Cummings 1994). Most artificial reef colonization studies have focused on structures located in shallow coastal waters, where movement between adjacent reefs, while a confounding factor, is not only likely but also nearly inevitable. Analogously, movement of adult reef fishes between shallow-water platforms is plausible because the distance between platforms is relatively small (0.1 to 10's of km) and surrounding water depths (15 – 21 m) are well within the physiological constraints of most reef fishes. Farther offshore, movement

between deep-water platforms (water depths > 100's of meters) separated by distances measured in > 10's of kilometers becomes far less likely for reef-dependent species, many of which show a high degree of 'site fidelity' (Matthews 1985). Recruitment from the plankton then becomes the primary means of colonization, and observations based on the supply of individuals can potentially reveal the degree to which these artificial reef habitats are biologically connected.

Because nearly all reef populations are dependent upon planktonic eggs and larvae for persistence, recruitment to artificial reef structures is subject to at least two major constraints: the availability of appropriate habitat, and successful settlement from local or distant sources (Bohnsack et al. 1994; Caselle and Warner 1996). Basic descriptions of the distribution, abundance, and seasonal occurrence of larval reef fishes are needed for the management of these stocks, and to better understand the functional role these artificial reefs play in the northern Gulf.

The objectives of this study were to document the diversity and abundance of tropical ichthyoplankton being supplied to four geographically distinct platforms and to compare the ichthyoplankton supply of these geographic areas to other ichthyoplankton assemblages in the Gulf and Caribbean. Specific hypothesis tested to achieve these objectives were (1) the distribution, abundance, and taxonomic composition of tropical ichthyoplankton does not vary with geographic location, time of day, season, or collection method; and (2) reef-fish recruitment can be inferred from the observed ichthyoplankton supply patterns.

Methods and Materials

The study was conducted from four platforms located in the northern Gulf, three of which lay along a cross-shelf transect from Grand Isle, Louisiana, out past the 200 m isobath (Fig. 1). The near-shore platform (Exxon's South Timbalier 54; ST54) was located approximately 32 km southwest of Grand Isle, at 90.417° W, 28.833° N, in 20 m of water. A mid-shelf platform (Mobile's Grande Isle 94A; GI94) was located 64 km south of Grand Isle, at 90.098° W, 28.526° N, in 61 m of water. On the shelf-break, one of the deep-water platforms (Mobile's Green Canyon 18; GC18) was located approximately 160 km southwest of Grande Isle, at 91.029° W, 27.943° N, in 230 m of water. In addition to these three platforms, a second shelf-break platform in the northwestern part of the Gulf was also sampled. British Petroleum's East Breaks 165 (EB165) was located 165 km south-southeast of Galveston, Texas, at 94.323° W, 27.819° N, in 245 m of water.

The biofouling communities differed among platforms, following closely the biotic structure and zonation descriptions of platform communities presented by Gallaway and Lewbel (1982) and Rezak et al. (1985). The near-shore community at ST54 was dominated at the surface by acorn barnacles (*Balanus reticulatus*), interspersed with thick concentrations of green algae (*Enteromorpha* sp.) and hydroids. At depths of -3 to -6 m, sea anemones (*Aiptasia* spp.) and bryozoans replaced the algae and hydroids within the barnacle mat, with live barnacles disappearing below -10 m. Hydroids, bryozoans, and encrusting sponges dominate below -10 m.

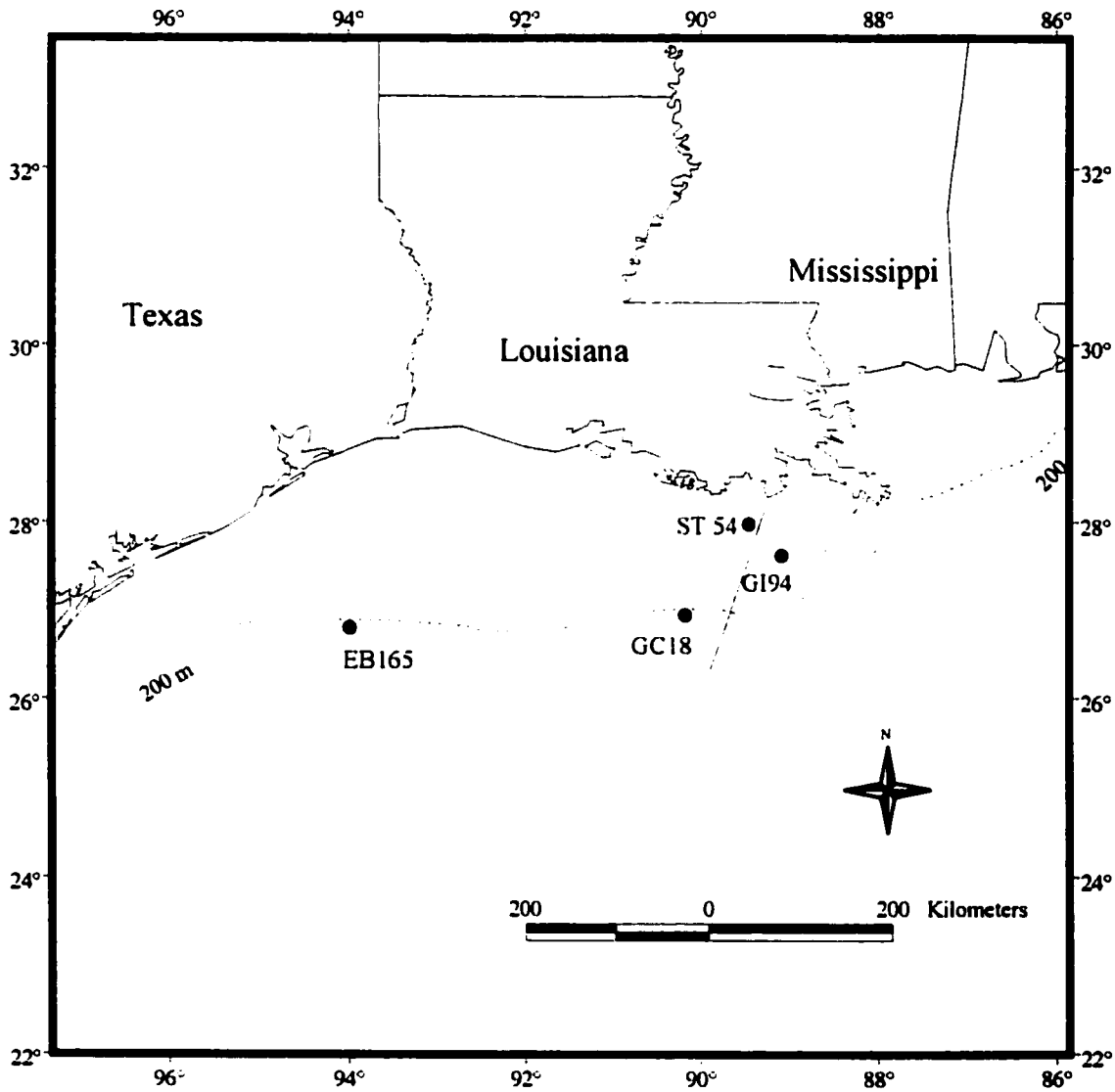


Figure 1. Location of platform artificial reef collection sites within the northern Gulf of Mexico. Solid diagonal line indicates the cross-shelf transect from Grand Isle, LA to the continental shelf break.

At GI94, barnacles (*Balanus* spp. and *Megabalanus* spp.) also dominated the surface community, although numerous bivalves (tree oyster *Isognomon* sp., sponge oyster *Ostrea* sp., and spiny jewel box *Chama* sp.) were also present. Leafy algae (*Ectocarpus* spp., *Polysiphonia* spp., *Jania* spp., and *Gelidium* spp.) were more prevalent at the mid-shelf platform, due to increased water clarity. Hydroids, bryozoans, and sea anemones dominated the fouling mat down to -30 m, with small patches of live corals (*Astrangia* sp. and *Tubastraea* sp.) common on the undersides of the structural cross-members. Denser colonies of encrusting sponges and alyconarians (*Carijoa riisei* and *Telesto* spp.) were also abundant to -30 m. Mobile invertebrate assemblages were dominated by brittle stars, urchins (*Eucidaris tribuloides* and *Echinometra* spp.) and polycheates (including the tropical *Hermodice carunculata*).

On the shelf-break platforms, more tropical invertebrate forms were commonly encountered, with stalked barnacles (*Lepas* spp.) commonly found among the surface mat of *Megabalanus* spp., bryozoans, and algae. Hydroids, pelecypods, alyconarians, and large encrusting sponge colonies dominated the fouling mat down to depths of -30 m. Long-spine urchins (juvenile *Daidema antillarum*) and spiny lobsters (*Panularis argus*) were frequently found on the shelf-break platforms. Below depths of -30 m, Atlantic thorny oysters (*Spondylus americanus*) and wire coral (*Cirrhipathes* sp.) were routinely encountered.

Reef fish families were categorized into two functional groups, reef-dependent and reef-associated, based loosely on the ecological distinctions presented by Choat and Bellwood (1991). The reef-dependent families included Serranidae (sea basses and

groupers), Chaetodontidae (butterflyfish), Pomacanthidae (angelfish), Pomacentridae (damselfish), Scaridae (parrotfish), Labridae (wrasses), and Acanthuridae (surgeonfish). Each family shares the characteristic of being found in close association with a reef habitat for their entire post-settlement life cycle. Reef-associated families (those families found around structures, and/or adults capable of movements between reef habitats) included Muraenidae (morays), Holocentridae (squirrelfish), Priacanthidae (bigeyes), Apogonidae (cardinalfish), Malacanthidae (tilefish), Carangidae (jacks), Lutjanidae (snappers), Gerreidae (mojarras), Haemulidae (grunts), Mullidae (goatfish), Ephippidae (spadefish), Opistognathidae (jawfish), Blenniidae (blennies), Gobiidae (gobies), Balistidae (leatherjackets), and Tetraodontidae (puffers).

Although the carangids are normally characterized as a transient piscivorous predator not strictly associated with the reef, they are a dominant member of many platform ichthyofaunal communities (Stanley and Wilson 1997). Because the carangids were especially abundant at both deep-water platforms on the shelf-break, I chose to include them in the reef-associated functional group.

Ichthyoplankton sampling has historically been conducted from a moving vessel with a wide variety of net designs (Powlik et al. 1991). Conducting equivalent quantitative sampling from a stationary platform presents challenges not encountered with traditional methods. Instead of moving nets through the water and actively filtering out organisms, stationary sampling relies on surface currents bringing organisms to the net. For this study, a passive-method, stationary plankton net with supplemental light aggregation devices was used to investigate the diel patterns of reef-

fish recruitment. The passive surface net consisted of a conical plankton net (3:1 aspect ratio, 60 cm mouth opening, 0.505 mm nitex mesh) suspended within a weighted, aluminum frame. The net-frame was deployed from the lower deck of the platform by a series of pulleys, which positioned the opened net horizontally into the oncoming surface current. By fishing only the upcurrent side of the platform, I assumed all the ichthyoplankton collected represented an accurate reflection of the diversity of fishes being supplied to the platform habitat, and not individuals that had come from the platform. Sample depths ranged from -1.5 to -4 m.

Surface net collections were taken seasonally from November 1994 to July 1997. Winter season collections were taken from December - February; spring season from March - May; summer season from June - August; and fall from September - November. Because this project was conducted in conjunction with other platform research programs, seasonal sampling periods were not uniform for each platform. Opportunities to occupy a sampling platform were contingent upon cooperation and permission from the production company and crew, and occasionally I either was delayed or denied access due to conditions beyond my control.

Initially, triplicate ichthyoplankton samples were collected on a diurnal schedule (dawn, noon, dusk, and midnight) from GC18, but sampling protocol was later refined based on the observed catch rates. Surface net collection results from GC18 during 1994 and 1995 indicated that reef-dependent larval fish abundance was lowest during the midnight period (see Results, Fig. 10) and samples from noon and dusk were statistically the same. Based on these initial results, sampling for the remainder of the

study (1996 and 1997) was conducted during consecutive dawn and dusk periods over several days (typically 3-4 days / trip).

The passive surface net was fitted with a General Oceanics flowmeter in order to calculate sample volumes. Fish densities are adjusted for the volume of water filtered and expressed as standardized numbers of fish / 100 m^3. Missing flowmeter readings were estimated with standard methods (Smith and Richardson 1977). Sampling duration was adjusted to compensate for the velocity of the surface current, with a target goal of approximately 200 m^3 water filtered for each sample. All samples were immediately fixed in 95% ethanol, and transferred within 48 hours to fresh ethanol for final storage.

During the winter, spring, and summer seasons of 1994 and 1995, surface net collections at GC18 were supplemented with light trap collections from the surface and a depth of -20 m. The -20 m depth stratum was chosen because this depth provided the first substantial horizontal structure beneath the platform. At this level, numerous drill pipes pass through a "template" or pipe guide/support that creates a semi-continuous, horizontal shelf. This horizontal structure accumulates much of the detrital particles falling from the platform legs, thus creating a "false bottom" microhabitat complete with a thin layer of biogenic sediments. This structure has the effect of baffling the current flow through the middle of the platform, creating lower velocities for light trap sampling. Because diver observations showed that many juveniles and adults of reef-fish species were typically found at higher abundance in close proximity to these templates, I fished the deep light trap in this area.

A quatrefoil trap design, similar to the design reported by Cope et al. (1996) was used as the light-aggregating device. The trap was illuminated with a 9.0-volt, halogen bulb, Ikelight underwater dive light. The trap was lowered along a cable anchored to the -20 m horizontal template, and allowed to fish the area immediately above the template. Surface light trap sets were fished under the middle of the platform, approximately 1 - 2 m's below the surface swell. Set times for both light traps were approximately 40 to 80 minutes and all collections were made concurrent with the surface net collections during the dusk to midnight periods. Power supply for the light source (C-cell batteries) were replaced after each set to ensure a consistent light levels. At the end of each light trap set, the trap was lifted onto the platform, its contents were drained through a cod-end piece (0.3 mm mesh net) and the sample immediately preserved in 95% ethanol. Light trap catches were standardized to a catch per unit effort (CPUE) by the following formula: total catch of larvae (sum of all families) divided by the sampling time in minutes, multiplied by 60 to standardized to a 1 hour trap set.

Once it became apparent that the light traps were not collecting larvae in numbers comparable to the surface net (see Results; 1994 and 1995 - Light Traps), an alternative light aggregating device was utilized for the remainder of the study. Using the same underwater dive light as an illumination source, three dive lights were attached to the outside of the net-frame at the mouth of the plankton net and the lighted plankton net (LPN) was fished identical to previous surface collections. Triplicate samples (lighted and unlighted) were collected from each dusk sampling

period for the remainder of the study. I utilized a random number table in order to determine the sampling order of the lighted and unlighted collections. Lighted plankton nets were deployed from EB165, GI94, and ST54 during the spring, summer, and fall seasons of 1996 and 1997, except for summer 1996 at ST54 and the spring 1997 at EB165.

Light traps, and later lighted plankton nets, were used with the assumption that certain fish larvae show a positive phototaxic response, and have the ability and willingness to swim to and enter an illuminated enclosure (Brogan 1984). Although physical factors such as water clarity and currents speed can effect larval fish catch efficiency and sample accuracy (Milicich et al. 1992), light traps have been shown to be an effective means of collecting larger larvae that can avoid conventional nets (Doherty 1987b; Victor 1991a; Mundy 1998). The capture of competent fish larvae (i.e., settlement stage individuals) with light attracting devices have been shown to be significantly correlated with the density of earlier stage larvae in the plankton as determined by conventional tows (Victor 1986a).

In the laboratory, all fish larvae were separated from whole collections and identified to family level, enumerated, and measured to the nearest 0.1-mm length with an ocular micrometer. While it is desirable to identify all fishes to the species level, a coarser level of taxonomic resolution may be appropriate, if the higher taxonomic level reflects the larger-scale pattern under study (Powles 1975; Vascotto 1976; Clarke and Warwick 1994). For collections containing a large number of individuals (> 30) of a particular family, a subsample of 30 randomly-selected individuals were removed with a

Hinson-Stimple volumetric pipette and measured to the nearest 0.1 mm length. Larval identifications were confirmed with published works (Randall 1968; Fritzche 1978; Johnson, 1978; Martin and Drewery 1978; Johnson and Keener 1979; Kendall 1979; Houde 1981; Fahay 1983; Leis and Rennis 1983; Richards 1984; Moser et al. 1984; Kelley et al. 1986; Leis and Trnski 1989; Baldwin 1990; Richards 1990; Ditty and Shaw 1994; Richards et al. 1994; Moser 1994; Kelley 1995; Farooqi et al. 1995), unpublished works, comparisons with preserved specimens from the reference collections at the Ichthyoplankton Laboratory at Louisiana State University, and taxonomic assistance by J. Ditty (National Marine Fisheries Service, Galveston, TX), D. Drass, and D. Hanisko (National Marine Fisheries Service, Pascagoula, MS). Representatives of each family were retained as voucher specimens.

During each sampling event (passive-method surface net, light traps, lighted plankton net), upper water column profiles of temperature (°C), salinity (parts per thousand), and dissolved oxygen (mg/l) were measured with CTD casts (data recorded at 5 m intervals to 20 m depth from ST54 and GI94; 10 m intervals to 30 m depth at GC18; surface water measurements only from EB165). Current direction and velocity profiles (cm/sec) were also measured with an Inter-Ocean Model S-4 current meter attached to the CTD.

Statistical Analysis

The experimental design was intended to be a factorial analysis of variance (ANOVA) comparison of the supply of reef fish larvae to artificial reef habitats, comparing platforms, seasons, and sampling times, adjusted for the continuous

environmental variables of temperature, salinity, and dissolved oxygen concentration. Correlations of ichthyoplankton family richness (total number of families / sample) and total larval fish density (N individuals / 100 m^3) with each environmental parameter were examined with linear regressions to determine any explanatory factors. Significant linear trends associated with dissolved oxygen concentrations were initially included as a covariate in the two-factor ANOVA (see below) of both family richness and total larval fish density, and in each case, the continuous covariate explained the smallest portion of the model sums of squares. Given the conflicting nature of the associations between dissolved oxygen concentrations and each dependent variable (negative for family richness and positive for total density), and the weak explanatory nature of these associations (linear regression model R^2 ranging from 0.02 to 0.04; see Results, Figures 3 and 4), inclusion of dissolved oxygen concentration as a covariate was deemed unnecessary. Unless otherwise noted, dependent variables were first transformed as $Log_{10}(N + 1)$ prior to analysis.

Surface net sampling conducted at GC18 during 1994 and 1995 consisted of a two factor ANOVA (Sokal and Rohlf 1981) to assess seasonal differences (fixed factors) in larval supply collected on a diurnal schedule (dawn, noon, dusk, and midnight, also fixed factors). Significant main effect factors were compared with an *a posteriori* Ryan-Einot-Gabriel-Welsch (REGWQ) multiple stage test (SAS 1999). The REGWQ procedure is the most powerful multiple stage available to control the maximum experiment-wise error rate (Ramsey 1978).

The experimental design for sampling at all four platforms in 1996 and 1997 consisted of a nested-factorial experiment, using a mixed-model ANOVA. Each platform (random factor) was sampled for 3-4 consecutive days (random factor) during each season (fixed factor). Sampling at dawn and dusk (fixed factors) over multiple days within each season represented a restriction on randomization, so sampling times were nested within days, and consecutive sampling days were nested within seasons. A tabular explanation of the expected mean squares and proper F tests associated with this model can be found in Appendix A. The only effect that lacked an exact F test was the season main effect, and it was found by a linear combination of mean squares, following the methods described in Hicks (1993).

Light trap collections at GC18 in 1994 and 1995 were compared with an unequal variance t test. Lighted plankton net collections at EB165, GI94, and ST54 during 1996 and 1997 were compared with a factorial ANOVA. Due to numerous missing cells within a fully developed, 3-way design (platform, N = 3; season, N = 4; and light, N = 2), I chose to assess seasonal and platform differences with a two-way mixed model. Platforms sampled during a common season (EB165, GI94, and ST54 during summer) were analyzed for differences in the amount of total ichthyoplankton, reef-dependent larvae, and reef-associated larvae being supplied over consecutive dusk sampling periods. Day-to-day variations were not considered. Any effect the light aggregating device (fixed factor) had on catch rates was tested as a main effect, as well as its' interaction with the platform main effect (random factor).

All dependent variable residuals were assessed for normality with normal probability plots, box-plots, and the Shaprio-Wilks test (*W*:Normal; SAS 1999). When non-normal residuals were encountered, Levene's test (SAS 1999) was performed on main effects to identify which factor(s) accounted for any heterogeneous variance. Additionally, Type III sums of squares were utilized for all tests, with an alpha value for rejecting the null hypothesis set at 0.05.

The power, or the probability of correctly rejecting the null hypothesis when it is false, of each ANOVA main effect test was determined with retrospective power analysis (Latour 1992). Effect size (defined as the absolute value of the maximum difference in group means, scaled by the within-population standard deviation, see Steidl et al. 1997) was calculated to determine the minimum number of samples (or the least significant number, LSN) needed to detect a difference based on the model variance (Shaver 1993). Confidence intervals (± 95 %) of each power determination were also calculated. Power analysis results can be found in Appendix B.

Length-frequency distributions of the most abundant reef-dependent and reef-associated families were compared with Pearson's Chi-square test of independence (SYSTAT 1992). Comparisons are based on pooled data from each sampling platform, with length-frequencies tabulated to the nearest whole mm. When test results were identified as suspect due to sparse data (more than one-fifth of the fitted cell values < 5; see SYSTAT 1992), data were further aggregated into 2 mm length groups and reanalyzed. Light attraction devices (lighted plankton nets only) were also tested for their effectiveness in capturing ichthyoplankton with two-way contingency tables. Chi-

square tests were used to determine if larval densities varied among platforms between the collection methods (lighted vs. unlighted nets), as well as testing for differences in length-frequency distributions of the most abundant families collected with the two gears.

Results

The frequency of sampling by platform and season are shown in Table 1. Each season is well represented throughout the course of this study, although the fall period did received less overall effort (17.2% of the total vs. a range of 23.9% to 33.5% of the total for other seasons). The December 1994 effort at GC18 was designated as the fall season for the purpose of analysis because sampling took place during the first week of December (1 – 5 December) and an additional winter collection took place later within the same season (20 – 24 February 1995). The greatest percentage of samples overall were collected at GC18 (39.7%), which was the primary focus of the study during 1994 and 1995. Samples collected during 1996 and 1997 were more evenly distributed throughout the other platforms, with the largest percentage of the remaining samples collected from GI94 (38.3%).

A total of 346 samples (225 passive surface plankton net sets, 36 light trap deployments, and 85 lighted plankton net sets) collected a total of36,676 fishes representing 80 families. The number of families per sample ranged from 0 to 20, with an overall mean of 5.8 (standard deviation [SD] = 4.0). Total catch per sample ranged from 0 to 5,279 individuals, with a mean of 163.7 individuals / sample (SD = 622.81).

Table 1. Frequency of ichthyoplankton samples (Surface Net = surface passive-method net, Light Trap = surface and deep light traps combined, and LPN = lighted plankton nets) collected by season and platform.

Date		Season	Sampling Platform	Surface Net	Light Trap	LPN	% Total Samples
November	1994	Fall	EB165	15	-	-	4.34
December	1994	Fall	GC18	11	8	-	5.49
February	1995	Winter	GC18	12	8	-	5.78
April	1995	Spring	GC18	12	8	-	5.78
June	1995	Summer	GC18	12	8	-	5.78
November	1995	Fall	GI94	12	-	-	3.46
January	1996	Winter	GC18	15	4	-	5.49
January	1996	Winter	ST54	15	-	9	6.93
February	1996	Winter	GI94	2	-	-	0.01
April	1996	Spring	GC18	16	-	12	8.09
April	1996	Spring	GI94	15	-	9	6.93
June	1996	Spring	ST54	15	-	6	6.07
July	1996	Summer	ST54	18	-	12	8.67
August	1996	Summer	GI94	15	-	6	6.07
September	1996	Fall	GC18	6	-	-	1.73
November	1996	Fall	GI94	11	-	9	5.78
April	1997	Spring	EB165	9	-	9	2.60
July	1997	Summer	EB165	14	-	13	7.80

Total larval fish densities ranged from 0 to 3,928.2 individuals / 100 m^3, with a mean of 135.9 / 100 m^3 (SD= 468.8).

Passive-method surface net sampling filtered 37,190 m^3 of water, with a mean of 174.1 m^3 / sample (SD = 169.5). Outliers represented samples taken when a crewboat was tied to the platform and the propeller wash from the boat greatly increased the amount of flow recorded. Ignoring these analomous samples, mean volumes were lower but had markedly less variability (mean = 130.0 m^3, SD = 51.1). Although the average sample volume was lower than the target amount of 200 m^3, sufficient amounts of water were filtered to accurately extrapolate observed larval fish densities to reflect numbers per 100 m^3.

Catch Composition

Rank order of families based on total catch and mean catch per 100 m^3 is shown in Table 2. Larvae too small to be identified to family level, damaged larvae, or disintegrated larvae are combined and reported as unidentified. Clupeidae and Engraulidae are combined and reported as Clupeiformes. By total number, nine taxa made up greater than 95% of the catch (Clupeiformes, Myctophidae, Carangidae, Lutjanidae, Scombridae, Serranidae, Mugilidae, Gobiidae, and Cynoglossidae). Clupeids dominated the overall catch (83.7 % by number) and were also dominant in terms of average density (189.4 / 100 m^3, see Table 2). Clupeiformes were not included in any analysis because they are not a representative component of the platform community, but instead pelagic planktivores typically associated with coastal

Table 2. Rank order of all families (by total number collected, and mean density) collected from four platforms in the northern Gulf during 1994-1997. Engraulidae and Clupeidae are combined and listed as Clupeiformes, Unidentified eels are listed as Anguilliformes. Functional group designation: RD = Reef-dependent, RA = Reef-associated.

Family	Functional Group	Total Number	Mean Density (N/100 m^3)	Percent Total	Cumulative Percent
Clupeiformes		30672	189.43	83.63	83.63
Myctophidae		1011	5.48	2.76	86.39
Carangidae	RA	1007	10.88	2.75	89.13
Lutjanidae	RA	454	5.15	1.24	90.37
Scombridae		439	5.39	1.20	91.57
Serranidae	RD	427	4.88	1.16	92.73
Mugilidae		390	6.44	1.06	93.79
Gobiidae	RA	351	2.28	0.96	94.75
Cynoglossidae		217	2.44	0.59	95.34
Unidentified / Damaged		211	1.77	0.58	95.92
Ophidiidae		161	5.09	0.44	96.36
Bothidae		155	1.41	0.42	96.78
Echeneidae		117	11.24	0.32	97.10
Gonostomatidae		103	1.35	0.28	97.38
Ophichthidae		92	1.73	0.25	97.63
Balistidae	RA	78	4.59	0.21	97.84
Sciaenidae		78	2.38	0.21	98.06
Pomacentridae	RD	63	1.42	0.17	98.23
Synodontidae		57	1.90	0.16	98.38
Bregmacerotidae		53	2.65	0.14	98.53
Opistognathidae	RA	45	3.64	0.12	98.65
Gadidae		42	2.39	0.11	98.76
Blenniidae	RA	32	1.70	0.09	98.85
Paralepididae		32	1.10	0.09	98.94
Stromateidae		32	2.27	0.09	99.03
Exocoetidae		31	0.70	0.08	99.11

Table 2. (cont.)

Family	Functional Group	Total Number	Mean Density (N/100 m^3)	Percent Total	Cumulative Percent
Centriscidae		27	2.01	0.07	99.18
Coryphaenidae		23	0.85	0.06	99.25
Sparidae		23	1.92	0.06	99.31
Triglidae		22	1.20	0.06	99.37
Soleidae		16	1.08	0.04	99.41
Bramidae		13	0.75	0.04	99.45
Priacanthidae		13	0.61	0.04	99.48
Gerreidae	RA	12	0.92	0.03	99.52
Mullidae	RA	11	1.22	0.03	99.55
Muraenidae	RA	11	1.00	0.03	99.58
Trichiuridae		11	0.64	0.03	99.61
Sphyraenidae		10	0.69	0.03	99.63
Ceratiidae		9	0.60	0.02	99.66
Merluccidae		9	1.37	0.02	99.68
Apogonidae	RA	8	0.98	0.02	99.71
Hemiramphidae		8	0.70	0.02	99.73
Microdesmidae		8	0.70	0.02	99.75
Tetraodontidae	RA	7	1.08	0.02	99.77
Melanostomiidae		6	0.80	0.02	99.78
Clinidae		5	1.43	0.01	99.80
Kyphosidae		5	0.94	0.01	99.81
Melamphaidae		5	1.23	0.01	99.83
Pholidae		5	0.96	0.01	99.84
Scorpaenidae		5	0.72	0.01	99.85
Chaetodontidae	RD	4	0.74	0.01	99.86
Moridae		4	1.45	0.01	99.87
Pomacanthidae	RD	4	1.36	0.01	99.89
Scopelarchidae		4	2.46	0.01	99.90
Atherinidae		3	0.91	0.01	99.90
Congridae		3	0.48	0.01	99.91
Moringuidae		3	0.32	0.01	99.92
Sternoptychidae		3	2.16	0.01	99.93
Syngnathidae		3	0.64	0.01	99.94
Alepisauridae		2	0.93	0.01	99.94
Chaismodontidae		2	0.74	0.01	99.95

Table 2. (cont.)

Family	Functional Group	Total Number	Mean Density (N/100 m^3)	Percent Total	Cumulative Percent
Nomeidae		2	0.47	0.01	99.95
Notosudidae		2	0.30	0.01	99.96
Anguilliformes		1	0.87	0.00	99.96
Astronesthidae		1	0.33	0.00	99.96
Aulopidae		1	1.25	0.00	99.97
Bathylagidae		1	0.72	0.00	99.97
Belonidae		1	0.32	0.00	99.97
Centrolophidae		1	0.78	0.00	99.98
Ephippidae	RA	1	0.59	0.00	99.98
Holocentridae	RA	1	0.90	0.00	99.98
Istiophoridae		1	0.54	0.00	99.98
Labridae	RD	1	0.96	0.00	99.99
Lobotidae		1	0.32	0.00	99.99
Malacanthidae	RA	1	0.50	0.00	99.99
Melanocetidae		1	0.50	0.00	99.99
Polynemidae		1	2.59	0.00	99.99
Scaridae	RD	1	0.55	0.00	100.00
Total		36,676		100.00	100.00

and estuarine waters, and because their numerical dominance would potentially mask any underlying ichthyoplankton supply patterns.

The only numerically abundant reef-dependent family was Serranidae, comprising only 1.2 % of the total catch. Combining all reef-dependent families, this functional group comprised a very small portion of the total catch (1.4 %). Notably absent from the entire study was the reef-dependent family Acanthuridae. The reef-associated functional group also made up a small portion of the total catch, comprising only 5.5 %. Carangidae, Lutjanidae, and Gobiidae made up approximately 89 % of the 2,032 reef-associated individuals collected. Notably absent from the reef-associated group was the family Haemulidae.

In terms of density, echeneids ranked second (11.2 individuals / 100 m^3), followed by the carangids, mugilids, and myctophids (10.9, 6.4, and 5.5 larvae / 100 m^3, respectively). Of the top 10 families that dominated the ichthyoplankton in terms of density, only serranids represent the reef-dependent group. Although serranid mean density equaled 4.9 individuals / 100 m^3, the combined density of all reef-dependent families was only 1.6 individuals / 100 m^3. Three reef-associated families (carangids, lutjanids, and balistids) were noted in the 16 most abundant families. Reef-associated families were found, on average, at a higher density than the reef-dependent families (2.4 vs. 1.7 larvae / 100 m^3, overall), but both functional groups were typically found at very low numbers in the plankton.

Relationships among Surface Ichthyoplankton and Environmental Variables

Depth profiles showed that the surface waters were fairly homogenous from the surface to -5 m for both temperature and dissolved oxygen, with the freshwater signal of Mississippi River outflow seasonally evident at both ST54 and GI94 (Fig. 2). From -10 to -20 m depth, little variation existed in any of the three environmental parameters. No linear trend was found between family richness and surface water temperature (t = 0.37; df = 1, 183; p = 0.71; $R^2 < 0.01$) nor family richness and salinity (t = 0.03; df = 1, 183; p = 0.98; $R^2 < 0.01$). A negative relationship was found between family richness and dissolved oxygen concentration (t = 2.79; df = 1, 183; p = 0.01; R^2 = 0.04; Fig. 3). Residual analysis from each environmental variable regression showed that the residuals were not normally distributed (W:Normal values ranged from 0.88 to 0.89), although no obvious outliers or curvature was detected. Logarithmic transformation of the dependent variable did little to improve the distribution of the residuals or improve the overall model R^2.

Regressions of total ichthyoplankton density followed the general pattern identified by family-level richness. No relationship was found between total density and temperature (t = 0.80; df = 1, 183; p = 0.43; R^2 = 0.004) and a positive, albeit statistically weak relationship (R^2 = 0.02) was found between total density and dissolved oxygen concentration (t = 2.01; df = 1, 183; p = 0.06; Fig 4). A significant negative relationship was found between total density and salinity (t = 2.76; df = 1, 183; p = 0.01; R^2 = 0.05), although influence statistics ("DIFFITS" = >> + 2) showed

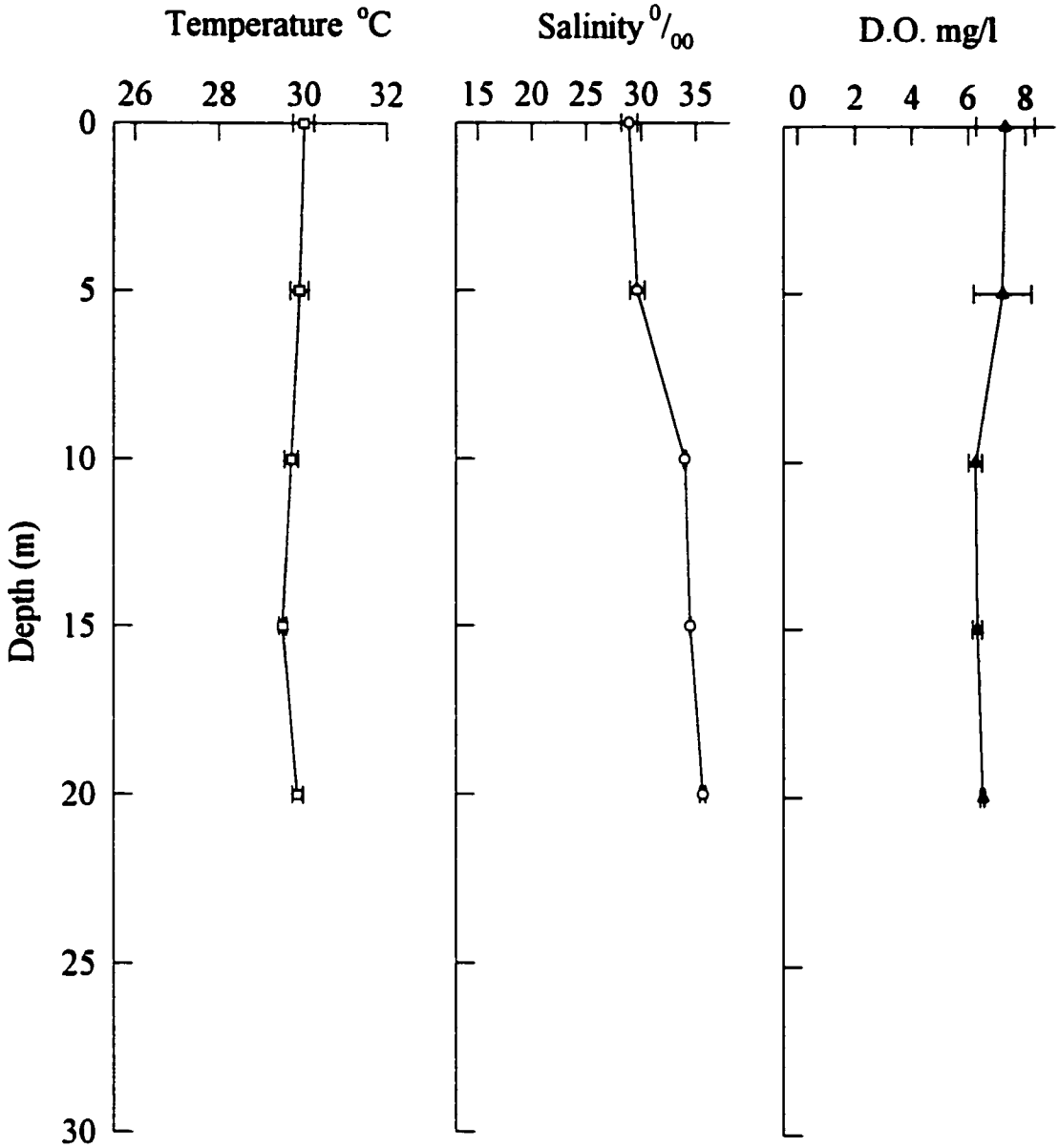


Figure 2. Synoptic view of the surface water physical characteristics at GI94 during the spring season in 1996. Error bars represent ± 1 SD.

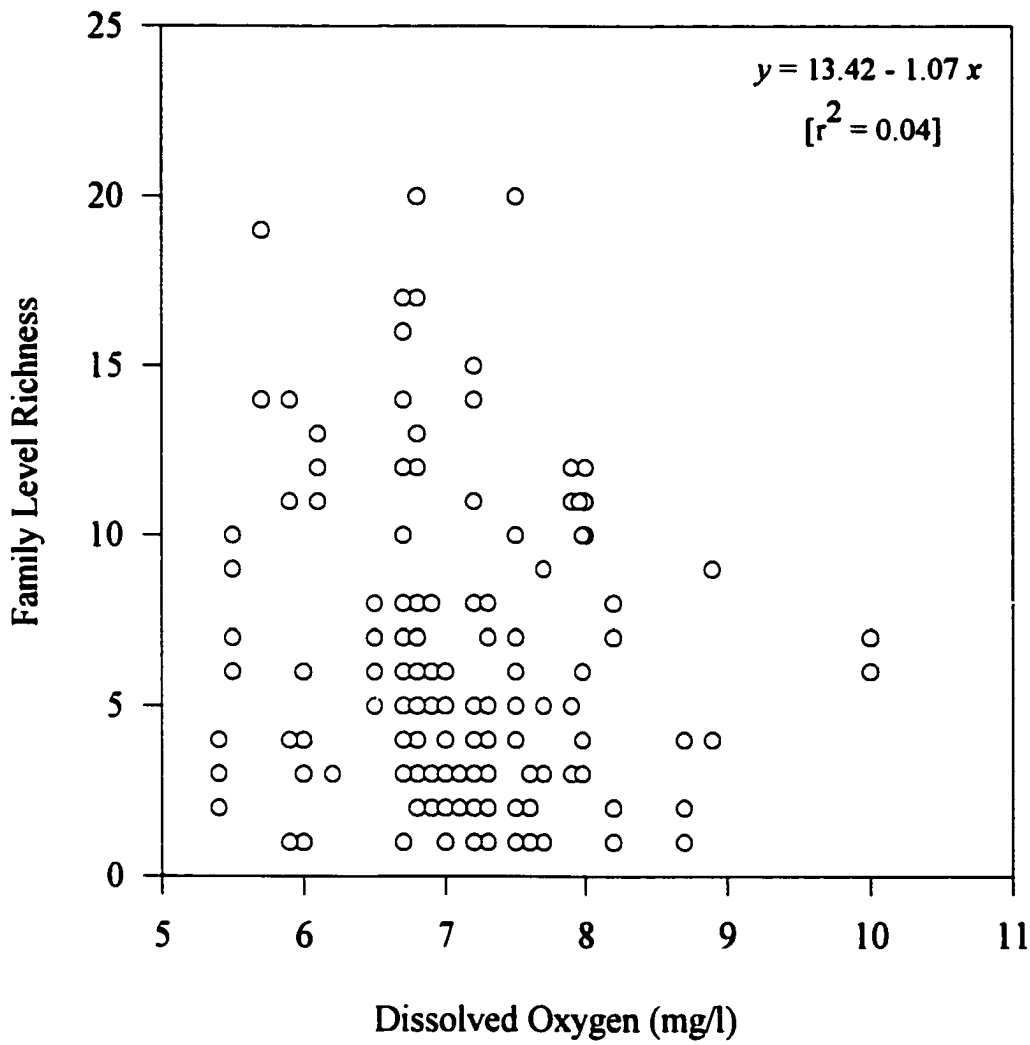


Figure 3. Relationship between family-level richness (Σ total numbers of families / sample) and surface water dissolved oxygen concentration at four artificial reef platforms in the northern Gulf.

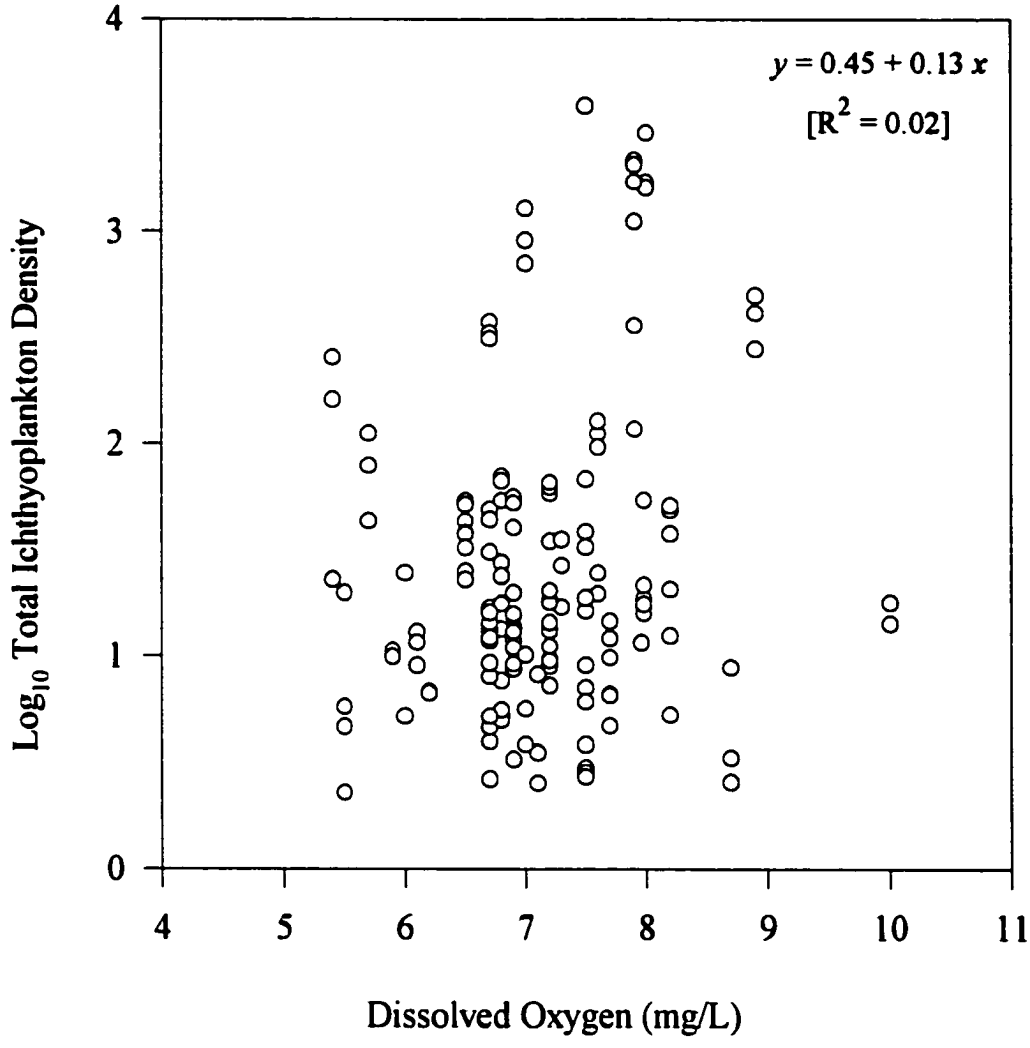


Figure 4. Relationship between Log_{10} transformed total ichthyoplankton density (Σ total number / 100 m^3) and surface water dissolved oxygen concentration at four artificial reef platforms in the northern Gulf.

that three summer season observations from ST54 had a large influence on the regression line (Fig. 5). Although water column profiles for salinity showed an obvious freshwater signal during this summer period (1996), a more prominent feature was the hypoxic-anoxic region in the lower portion of the water column (Fig. 6). During this sampling effort, surface water dissolved oxygen concentrations ranged from 4.8 to 6.5 mg/l, falling to 3.0 mg/l at -10 m depth. Below -10 m, hypoxic-anoxic conditions of < 2.0 mg/l to 0.0 mg/l were encountered. Removing the strong influence of these three samples revealed no significant relationship between total density and salinity ($p = 0.53$, $R^2 < 0.01$).

1994 and 1995 – Two Factor ANOVA Model

Family-Level Richness

At GC18, family richness ranged from a high of 20 families per sample during both the summer and winter seasons to a low of 2 families per sample during fall. Residual analysis satisfied the conditions of normality and the raw, untransformed values were used. The season × time of day interaction was significant ($F_{(9, 54)} = 5.27$; $p < 0.01$; Fig. 7), and accounted for the largest portion of the model sums of squares. Family richness greatly increased during both the dawn and noon sampling times during the summer season, nearly doubling the total family richness seen during winter and spring. Dusk and midnight sampling times during summer did not show a similar increase. Seasonally, the dusk and midnight sample periods generally increased from winter through the fall, with maximum family richness recorded during fall. Although

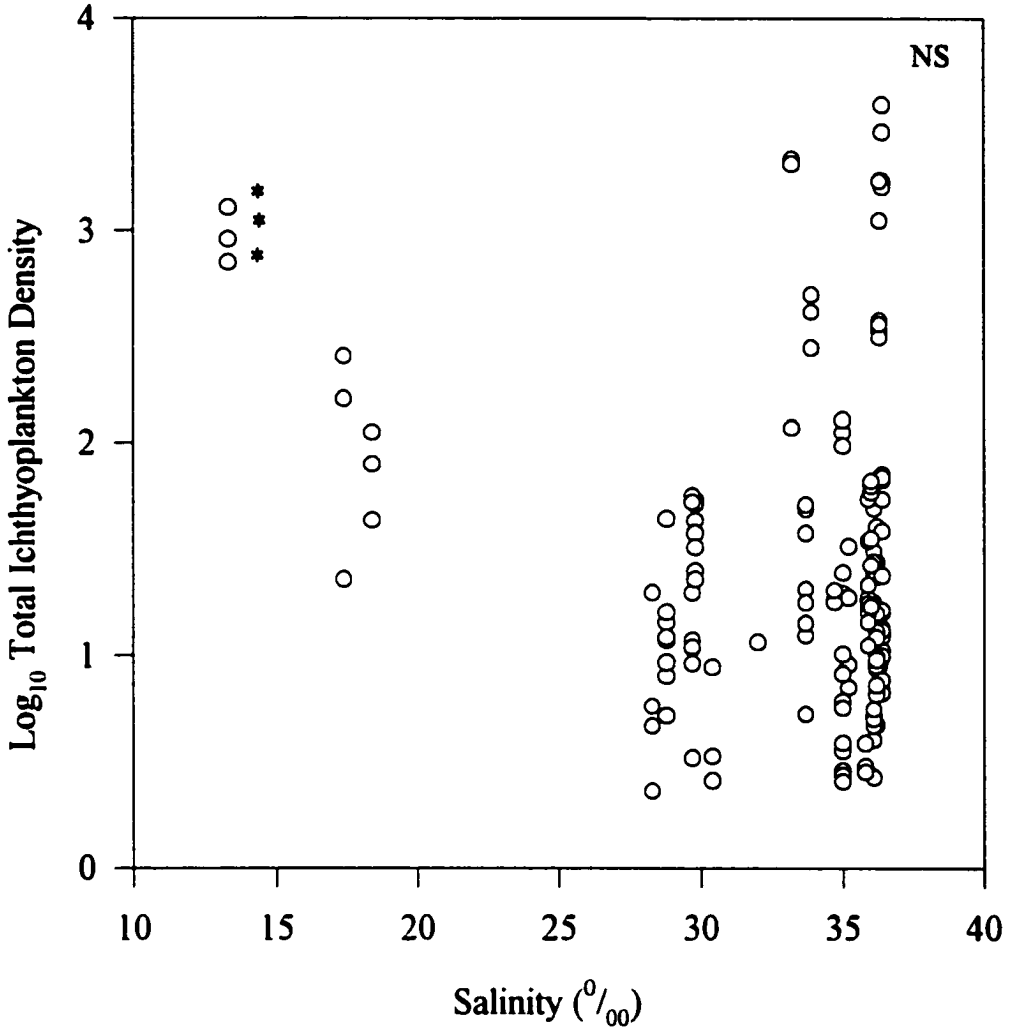


Figure 5. Relationship between Log_{10} transformed total ichthyoplankton density (Σ total number / 100 m^3) and surface water salinity at four artificial reef platforms in the northern Gulf. * = Influential observations (residual DIFFITS values >> +2).

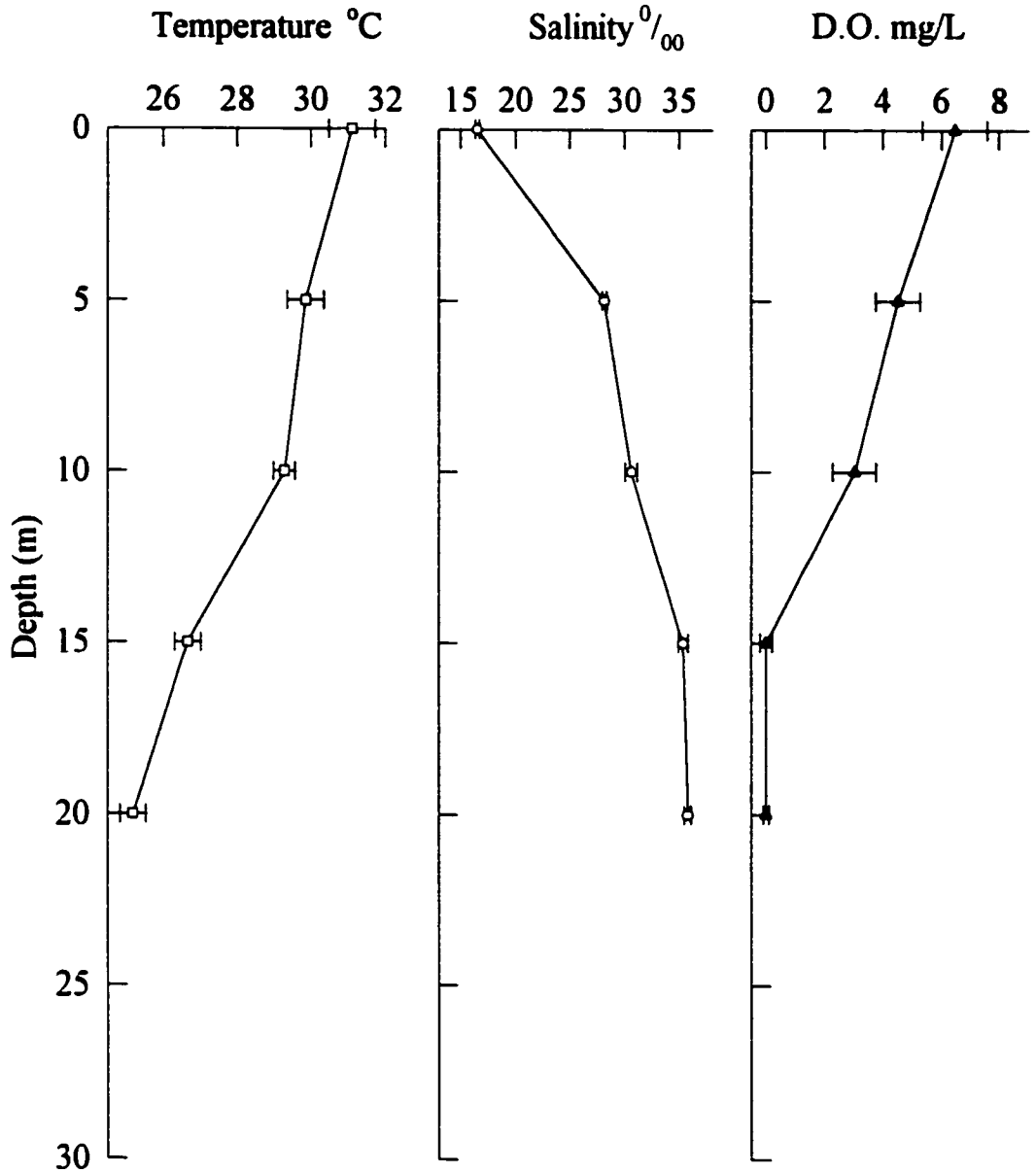


Figure 6. Water column profiles during the hypoxic event at ST54 during the summer 1996. Error bars represent ± 1 SD.

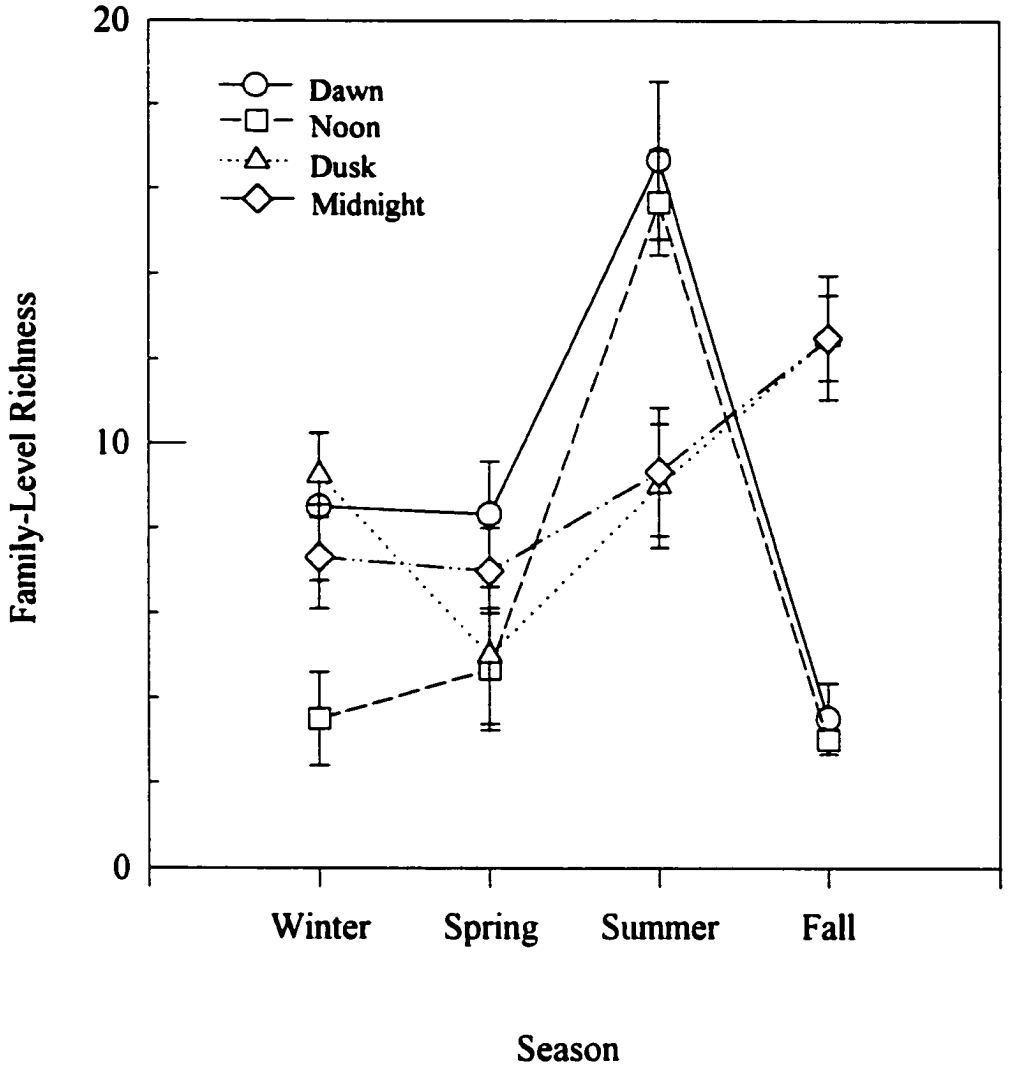


Figure 7. Family-level richness (Σ numbers of families / sample; ± SE) of ichthyoplankton collected seasonally with the diurnal sampling protocol at GC18 during 1994 and 1995.

mean family richness was not statistically different between sample times, family level richness was highest during the dawn and dusk periods.

Total Larval Fish Density

The total density of ichthyoplankton being supplied to GC18 was analyzed with the same factorial design ANOVA, and again seasonal effects explained the greatest amount of the variation. Average densities ranged from 1.7 fish / 100 m^3 during dusk in the spring, to > 1000 fish / 100 m^3 during dawn and dusk in the winter. Although both main effects were significant (Season main effect $F_{(3, 39)} = 14.32$; $p < 0.001$; Time of day main effect $F_{(3, 39)} = 13.46$; $p < 0.001$), the interaction term was also identified as significant as seen in Figure 8. Average densities during the dusk and midnight sampling times were quite similar throughout the first year of the study, with both having highest densities in the winter followed by a seasonal low in the spring. The dawn sampling time followed much of the same pattern, albeit with higher average densities, especially during the winter, spring and summer periods. The noon sampling time departed from the pattern of the three other diurnal periods, with the highest densities being recorded in the summer period. This dramatic increase was similar to the pattern identified for family richness measured at noon.

Although the time x season interaction term was significant, the REGWQ means test was performed on the sample time main effect to assess the diurnal sampling protocol. Two groups were identified, with the dawn and noon times similar in terms of the total amount of ichthyoplankton being supplied to the platform (Fig. 9).

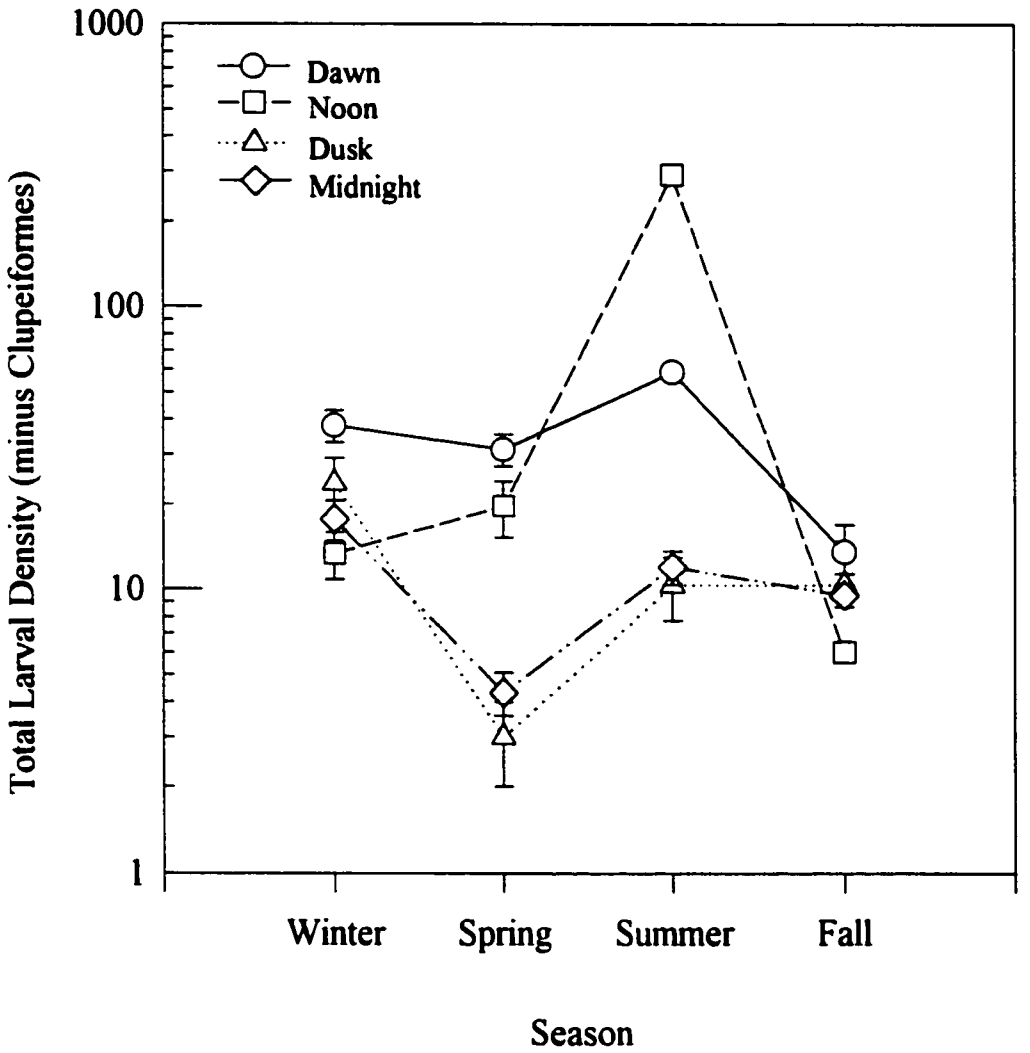


Figure 8. Mean density (total number minus Clupeiformes / 100 m^3; ± SE) of the total surface ichthyoplankton collected seasonally with the diurnal sampling protocol at GC18 during 1994 and 1995.

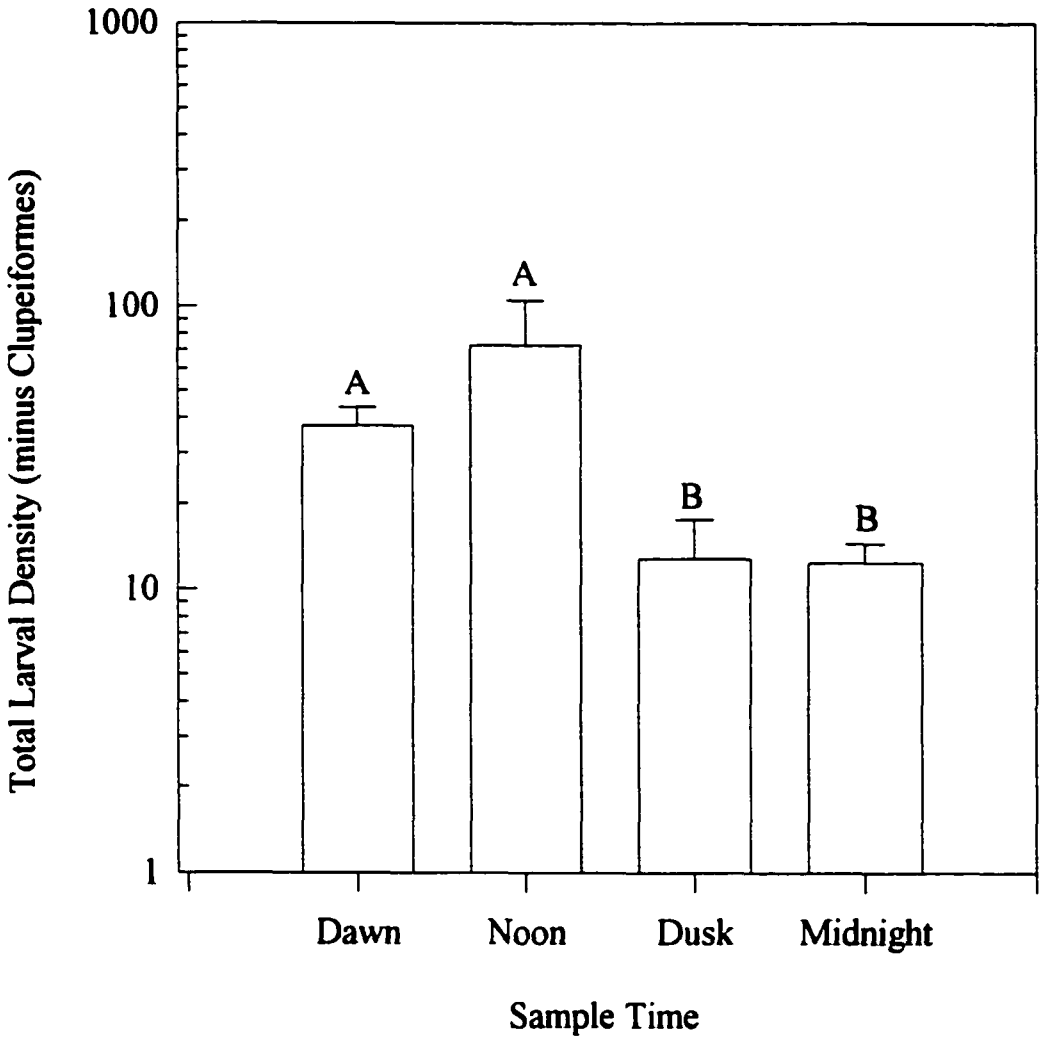


Figure 9. Mean density (total number minus Clupeiformes / 100 m^3; ± SE) of the total surface ichthyoplankton collected diurnally at GC18 during 1994 and 1995. Letters indicate the results of the REGWQ test where means with the same letter are not significantly different.

Reef-Dependent Supply

Densities of reef-dependent families averaged 0.8 larvae / 100 m^3, and ranged from 0 to 8.6 / 100 m^3. Of the total collection from GC18 during 1994 and 1995, a majority (70.9 %) was devoid of reef-dependent families. The low model R^2 (0.54) and high coefficient of variation (C.V. = 123.37) is reflective of this disparity of samples missing reef-dependent families. Their absence was not confined to any particular season or sampling time (Fig. 10). The significant interaction of season and sample time ($F_{(9, 54)} = 2.37$; $p = 0.03$) accounted for the greatest amount of variation (46% of the model sums of squares). No seasonality was identified ($F_{(3, 54)} = 2.12$; $p = 0.114$), although differences in sampling times were significant ($F_{(3, 54)} = 5.17$; $p = 0.004$).

Similar to total larval fish densities, the reef-dependent functional group was least abundant during midnight. The most abundant reef-dependent family, Serranidae, was caught primarily during dawn and noon sampling, whereas the pomacentrids were equally abundant from dawn and dusk (Table 3). No other family was caught in sufficient numbers to allow any clear diurnal supply patterns to be elucidated.

Reef-dependent residuals were not normally distributed (W:Normal = 0.78, $p < 0.001$), and Levene's test showed the variance among sampling times differed significantly ($F_{(3, 54)} = 3.20$; $p = 0.03$). Additional efforts to correct for the severe positive skewness associated with the abundance of zeros in the data set (a separate $(^1/_{[N + 1]})$ transformation; see Tabachnick and Fidell 1996) failed to substantially improve normality. Residual plots revealed that two values accounted for the majority of the

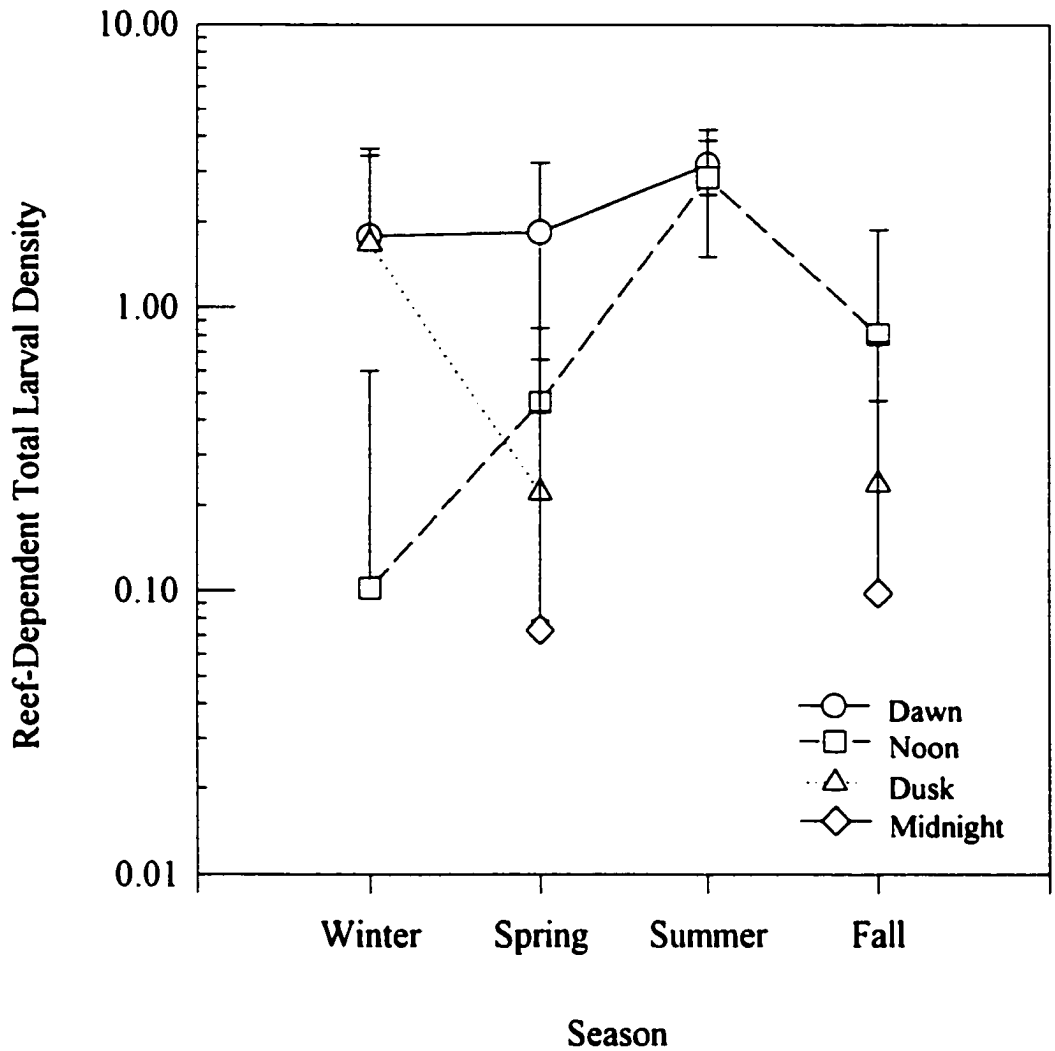


Figure 10. Mean larval density (Σ total number / 100 m^3; ± SE) of the reef-dependent functional group collected seasonally with the diurnal sampling protocol from GC18 during 1994 and 1995.

Table 3. Percent occurrence by family of the reef-dependent functional group collected with the diurnal sampling protocol at GC18 during 1994 and 1995. N = total number of larvae collected.

Family	Dawn	Noon	Dusk	Midnight	N	Percent Total
Serranidae	68.5	22.2	7.4	1.9	54	65.1
Pomacentridae	38.5	15.4	38.5	7.7	26	31.3
Pomacanthidae	100.0	0	0	0	2	2.4
Scaridae	0	0	100.0	0	1	1.2
Average Percent Total by Sample Time	59.0	19.3	18.1	3.6		

normality departure (studentized residual values of 4.65 and 3.91, respectively). These potential outliers corresponded to higher than expected densities collected during the dawn and dusk sampling times during the winter season of 1996.

Reef-Associated Supply

Reef-associated families were much more abundant than the reef-dependent families, averaging 14.13 fish / 100 m^3 vs. 0.84. Highest densities of reef-associated families were recorded during the summer (179.8 / 100 m^3, primarily carangids during the noon sampling time). Similar to the reef-dependent functional group, complete absences (approximately 20 % of samples) from the surface waters were also noted in fall, winter, and spring seasons. Significant seasonal differences were found in larval supply ($F_{(3, 48)} = 25.29$; $p < 0.001$), along with a significant interaction between seasonal and diurnal time main effects ($F_{(9, 48)} = 4.05$; $p < 0.01$, model $R^2 = 0.75$ and C.V. = 58.56). No diurnal differences were detected ($F_{(3, 48)} = 1.49$; $p = 0.23$; Fig 11), yet during summer and fall, individual families did appear to show diurnal supply patterns. Gobiids were caught primarily during the dusk and midnight periods, whereas Carangidae, Lutjanidae, and Balistidae were encountered at higher density during the day (Table 4). Carangids numerically dominated this functional group during the summer 1995 period by a factor of three. Other reef-associated families were also found in higher densities during the day (Gerreidae, Blenniidae, and Muraenidae), although each family contained only a few individuals and clear diurnal supply patterns were difficult to ascertain.

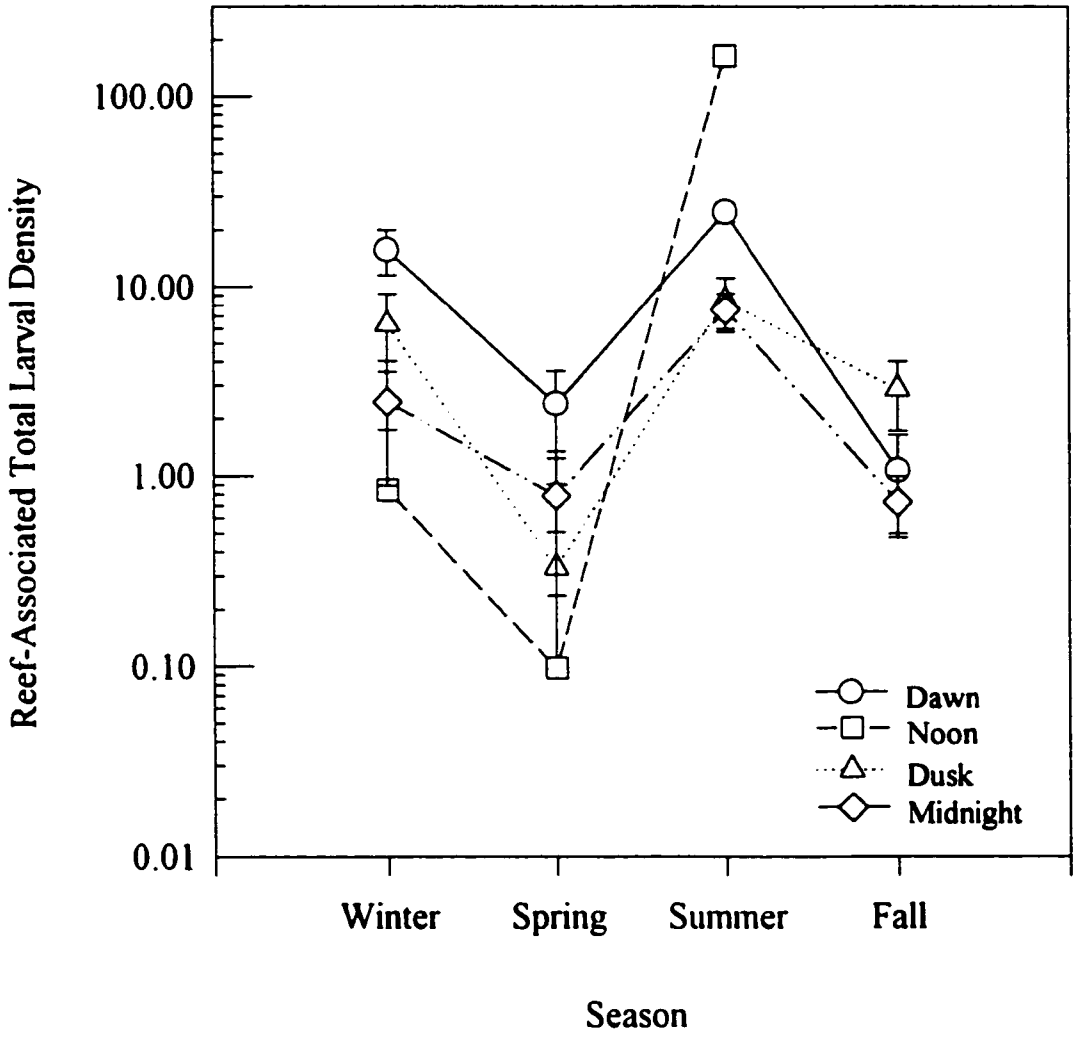


Figure 11. Mean density (Σ total number / 100 m^3; ± SE) of the reef-associated functional group collected seasonally with the diurnal sampling protocol from GC18 during 1994 and 1995.

Table 4. Percent occurrence by family of the reef-associated functional group collected with the diurnal sampling protocol at GC18 during 1994 and 1995. N = total number of larvae collected.

Family	Dawn	Noon	Dusk	Midnight	N	Percent Total
Carangidae	23.9	62.3	6.9	6.9	782	72.8
Gobiidae	8.8	2.2	56.0	33.0	91	8.5
Lutjanidae	43.5	42.4	9.4	4.7	85	7.9
Balistidae	72.4	23.7	3.9	0	76	7.1
Gerreidae	72.7	9.1	18.2	0	11	1.0
Blenniidae	50.0	33.3	0	16.7	6	0.6
Muraenidae	0	83.3	0	16.7	6	0.6
Priacanthidae	50.0	0	25.0	25.0	4	<0.5
Apogonidae	0	0	100.0	0	2	<0.5
Holocentridae	0	100.0	0	0	1	<0.1
Opistognathidae	0	0	100.0	0	1	<0.1
Tetraodontidae	0	0	100.0	0	1	<0.1
Average Percent Total by Sample Time	28.5	51.5	11.5	8.6		
Average without Carangidae	40.8	22.6	23.6	13.0		

The reef-associated group residuals were not normally distributed (W:Normal = 0.94, $p = 0.02$) and Levene's test showed significant differences for both sample times ($F_{(3, 48)} = 8.24$; $p < 0.001$) and seasons ($F_{(3, 48)} = 17.39$; $p < 0.0001$). Potential outliers accounting for this departure corresponded to the summer-noon sampling time, which was dominated by the large pulse of carangid and balistid larvae. These outliers produced studentized residual values ranging from 2.6 to 4.3.

The majority of reef-dependent families (77.1%) and a large percentage of reef-associated families (39.9%) were collected in the dawn and dusk samples. Excluding the anomalous carangid catch of 1995, the dawn and dusk sample times had similar totals of reef- associated (64.4% as compared to 77.1% reef dependent larvae).

1996 and 1997 – Nested ANOVA Model

Reef-Dependent Supply

The nested-factorial analysis of variance of both functional groups from all four study platforms during 1996 and 1997 showed that seasonal differences in ichthyoplankton supply was less significant than was the case at GC18 alone. For the reef-dependent functional group, ANOVA results revealed that neither main effect (platform and season) nor nested factors (day nested within season and time nested within day) differed significantly in terms of the number of larvae being supplied to the platforms, although the nested interaction terms were significant (Table 5). The average density of reef-dependent families was 2.1 individuals / 100 m^3 (SD = 5.5), ranging from 0 to 35.5 / 100 m^3 during spring 1997 at EB165. As was the case with

Table 5. Analysis of variance of Log_{10} transformed reef-dependent total density at all four platforms during 1996 and 1997. Brackets denote a nested term; see Appendix A for explanation of proper error terms. Pr > F, probability of obtaining a larger F value; * P < 0.05, ** P < 0.01, *** P < 0.0001.

Source	df	Type III SS	Mean Square	F Value	Pr > F
Platform	3	1.29	0.43	0.90	0.448
Season	3	0.06	0.02	1.43	>0.05
Platform×Season	6	1.05	0.17	0.36	0.880
Day(Season)	7	0.49	0.07	0.15	0.989
Platform×Day(Season)	7	3.35	0.48	8.75	0.0001 ***
Time(Day)	6	3.19	0.53	2.57	0.109
Platform×Time(Day)	8	1.66	0.21	3.79	0.0001 ***

reef-dependent families at GC18 alone, a large percentage of surface plankton samples were devoid of this functional group (65.4 % for 1996 and 1997, vs. 70.9 % for 1994 and 1995). Again, their complete absence from the surface waters was not confined to any particular season or sampling platform (Fig. 12).

Although not statistically significant, the largest portion of the model sums of squares was attributed to differences in larval supply associated with the nested sampling time factor (time doubly nested within day and season, Time(Day), See Table 5). Combined with the differences seen among the four platforms, the platform × nested time interaction term was highly significant (Fig. 13). The offshore platforms (EB165 and GC18) received the highest numbers of reef-dependent larvae, although there is no clear dawn / dusk pattern between the two. At EB165, reef-dependent larvae were more abundant during dawn, whereas at GC18, they were slightly more abundant at dusk. Both shallow water platforms (GI94 and ST54) had substantially less reef-dependent larvae supplied to them, and also showed greater dawn to dusk variation.

Residuals of the reef-dependent families were not normally distributed (W:Normal = 0.84, $p < 0.001$). A large number of potential outliers (17 samples identified) all corresponded to spring collections (April 1996 and 1997) from the deep-water shelf-break stations. Reef-dependent densities during these two periods exceeded the mean by factors ranging from 5 to 15.

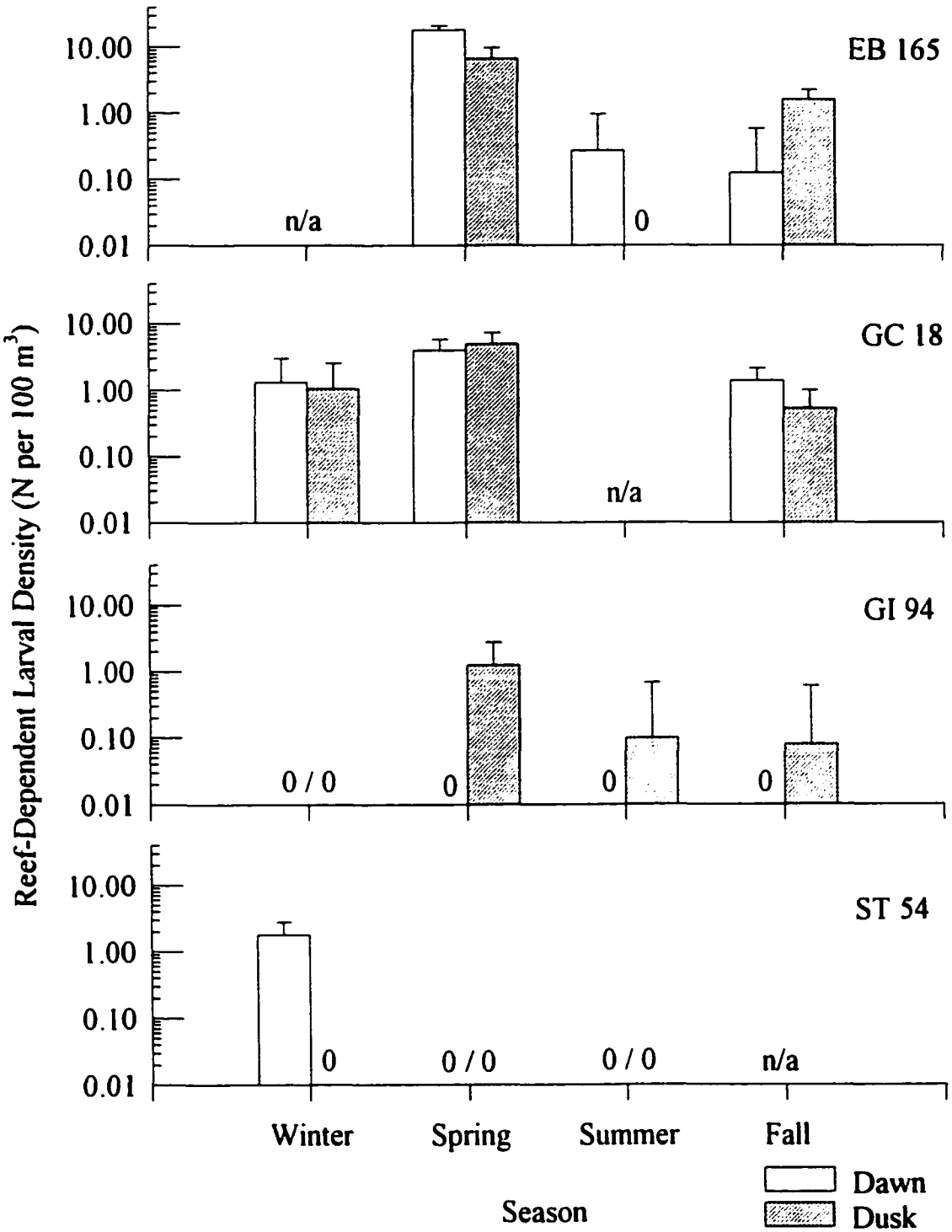


Figure 12. Mean total density (Σ total number / 100 m^3; + SE) of the reef-dependent functional group collected seasonally with the dawn-dusk sampling protocol from all four platforms. N/A represents seasons not sampled; 0 represents seasons sampled but zero catch recorded.

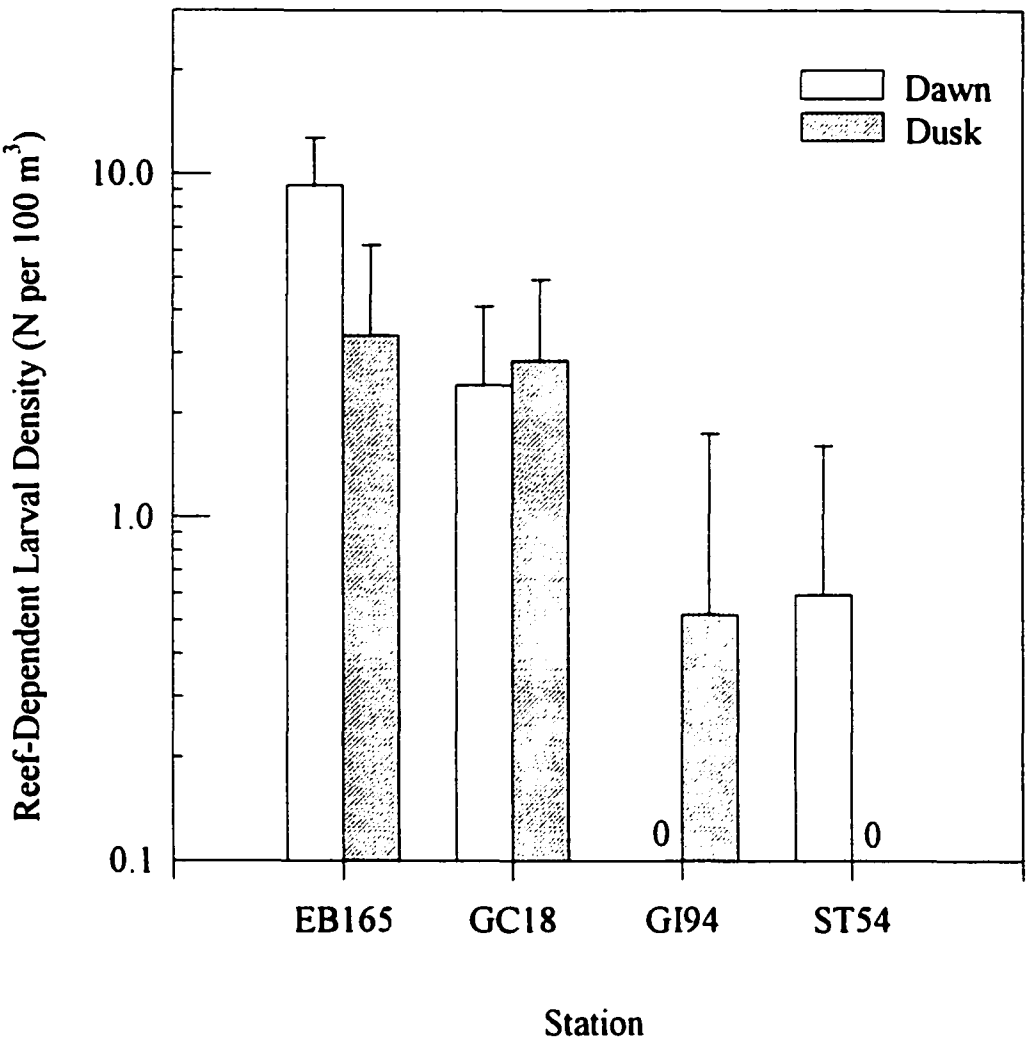


Figure 13. Mean density (Σ total number / 100 m^3; + SE) of the reef-dependent functional group (pooling across seasons) collected at dawn and dusk from each platform.

Reef-dependent density at all four platforms during 1996 and 1997 were again dominated by the serranids (Table 6). Although length-frequency distributions for both offshore platforms appear similar (EB165 median = 4.0 mm SL, SD = 0.86; GC18 median = 3.4 mm SL, SD = 1.24), the Chi-squared test revealed significant differences ($\chi^2 = 24.72$, N = 302, df = 8, $p = 0.002$; Fig. 14). More early stage larvae (< 3.0 mm SL), as well as a greater numbers of late stage, post-flexion individuals (>5.5 mm SL) were collected at GC18. The serranid supply to the mid-shelf platform was composed of similar sized individuals (3.0 to 5.5 mm SL), though in far fewer numbers. The coastal platform had the lowest numbers of serranids supplied, yet the largest individuals (> 10 mm SL) encountered.

Pomacentridae was the second-most abundant reef-dependent family collected. Their length-frequency distributions, among the three platforms where this family was collected, were not statistically significant ($\chi^2 = 13.16$, N = 55, df = 10, $p = 0.22$; Fig. 15). As adults, they are abundant members of the platform community at GI94, yet pomacentrid larvae were absent from the surface net collections over the course of this study.

Reef-Associated Supply

Reef-associated families were numerically more abundant than the reef-dependent functional group at each platform, although they still comprised a very small portion of the total ichthyoplankton in the surface waters. Densities ranged from 41.5 larvae / 100 m^3 during summer 1997 at EB165 to completely absent (76 of 159

Table 6. Numbers of larvae from the reef-dependent functional group, by family, collected at dawn and dusk from all platforms during 1996 and 1997. Percent Total = the contribution of each family to the total collection.

Family	Dawn	Dusk	Total	Percent Total
Serranidae	202	194	396	89.2
Pomacentridae	38	1	39	8.8
Pomacanthidae	4	0	4	0.9
Chaetodontidae	2	0	2	0.7
Labridae	0	1	1	0.3
Scaridae	0	1	1	0.3
Acanthuridae	0	0	0	0.0

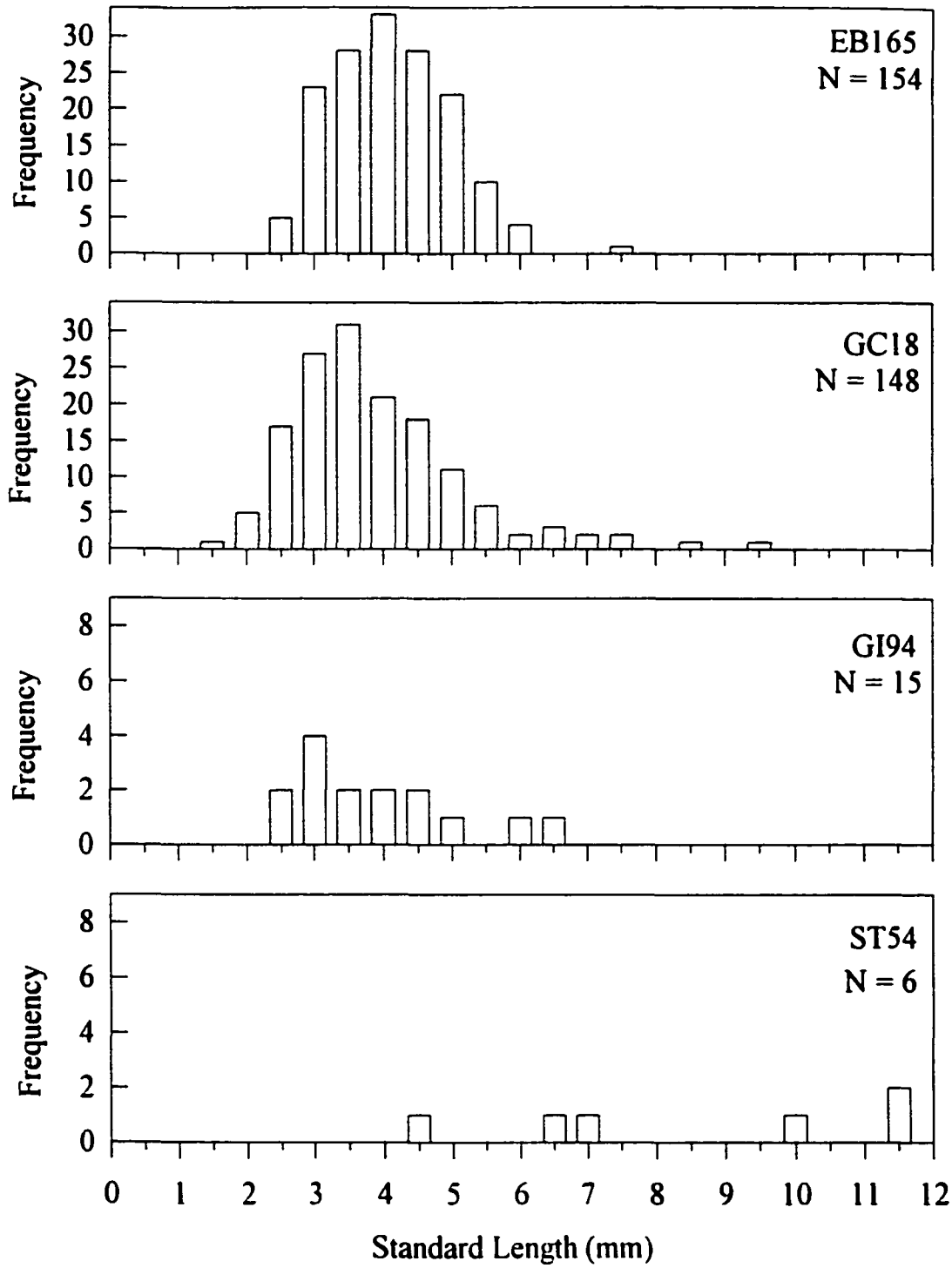


Figure 14. Length-frequency distributions (SL) of Serranidae larvae collected from each platform (all years 1994 - 1997). Note change in the *y*-axis between the offshore stations (EB165 and GC18) and the near-shore stations (GI94 and ST54). N = total number of individuals measured.

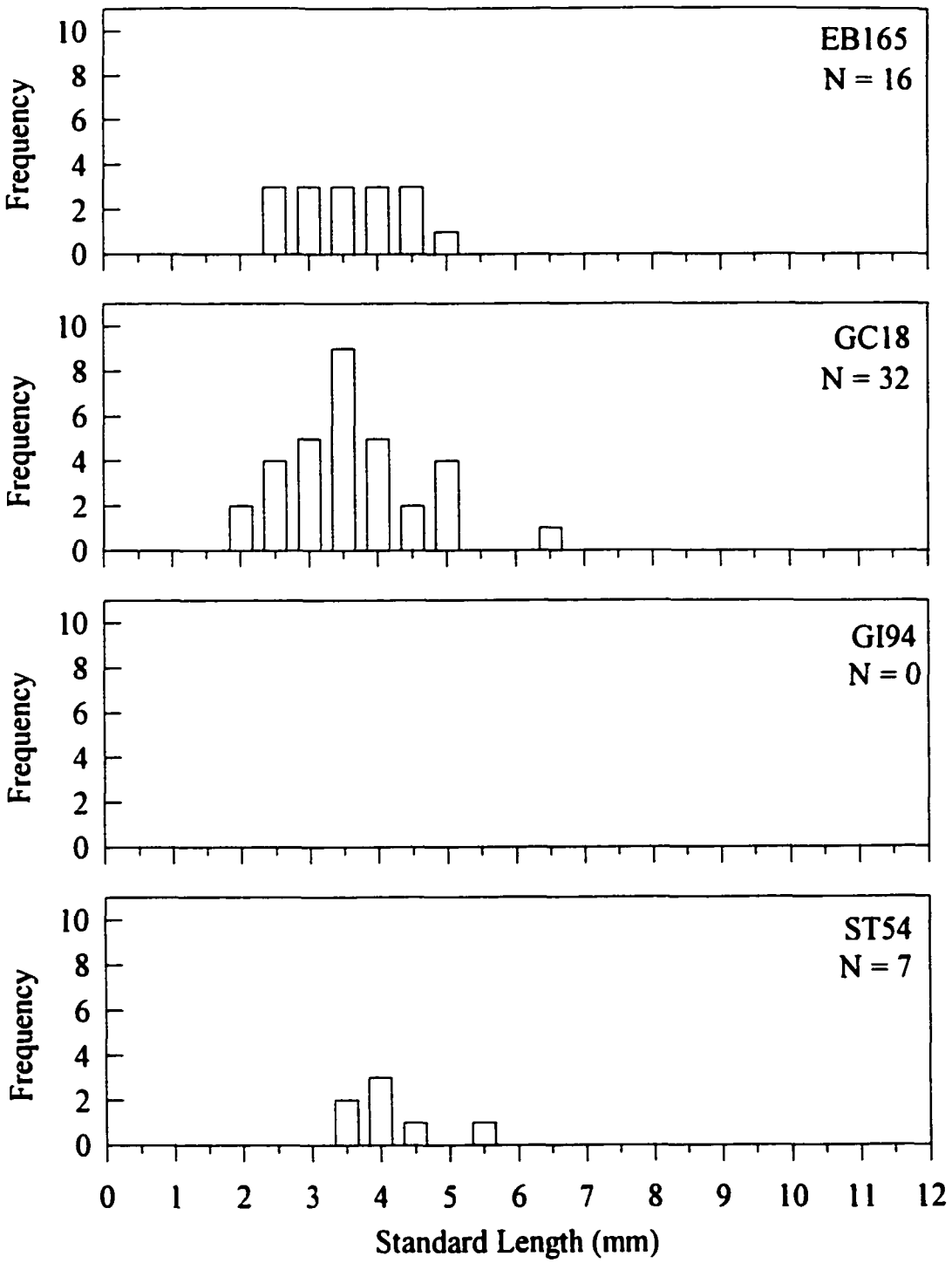


Figure 15. Length-frequency distributions (SL) of Pomacentridae larvae collected from each platform (all years 1994 - 1997). N = total number of individuals measured.

observations or 47.8%) during spring and fall from ST54 and GI94, respectively. Mean density for reef-associated families was 2.7 larvae / 100 m^3 (SD = 6.7), as compared to 2.1 for reef-dependent families.

The platform main effect, as well as the platform × season main effects interaction was identified as significant in the nested ANOVA model (Table 7). Day to day variations in reef-associated supply was not significantly different when averaged over all platforms, although the platform × nested day within season interaction term was identified as significant. Overall dawn to dusk differences in supply were absent, although the nested day within season × platform interaction was identified as significant.

The platform main effect differences identified by the REGWQ procedure showed an overlap of the offshore and mid-shelf platforms, with the GC18 clearly having greater densities than the coastal station at ST54 (Fig. 16). Although seasonal differences in supply were not significant, their interaction with the platform main effect was significant, accounting for the largest portion of the model sums of squares. The offshore platforms (EB165 and GC18) tended to have higher numbers of reef-associated families during all seasons except for spring, and this agreed well with the seasonal pattern identified from GC18 alone during 1994 and 1995 (see Fig. 10). The mid-shelf platform (GI94) had higher numbers of reef-associated supply during the winter and spring, with substantially lower numbers during in summer and fall. While the coastal platform (ST54) had the lowest numbers of reef-associated larvae being

Table 7. Analysis of variance of Log_{10} transformed reef-associated total density at all four platforms during 1996 and 1997. Brackets denote a nested term; format follows Table 5.

Source	df	Type III SS	Mean Square	F Value	Pr > F
Platform	3	3.78	1.25	8.49	0.010 *
Season	3	0.74	0.25	0.52	>0.05
Platform×Season	6	11.20	1.86	12.60	0.002 **
Day(Season)	7	0.69	0.09	0.66	0.701
Platform×Day(Season)	7	1.03	0.15	3.44	0.002 **
Time(Day)	9	0.44	0.05	1.13	0.346
Platform×Time(Day)	10	1.90	0.19	4.42	0.001 ***

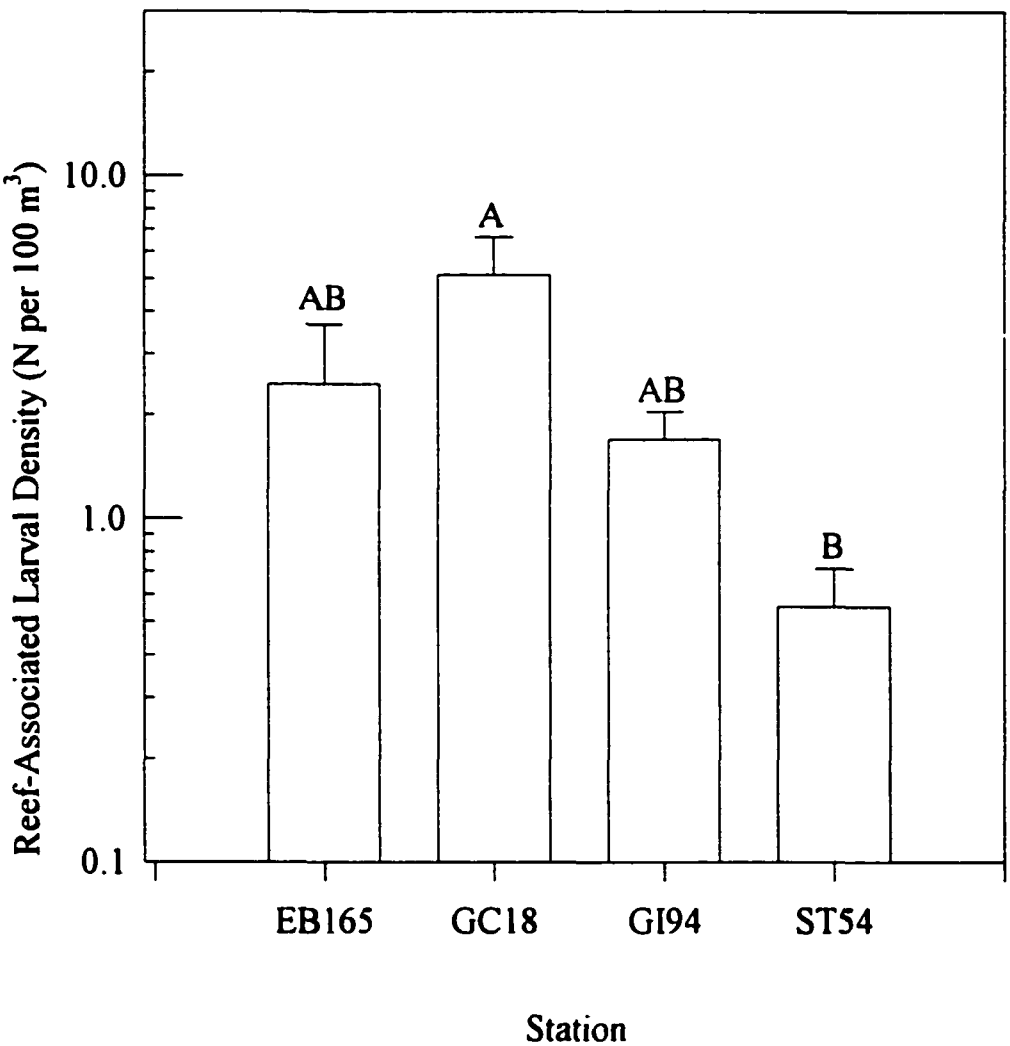


Figure 16. Mean density (Σ total number / 100 m^3; + SE) of the reef-associated functional group collected at dawn and dusk from each platform. Letters indicate the results of the REGWQ test where means with the same letter are not significantly different.

supplied during winter and summer, overall it was least variable in terms of larval supply.

The two nested interaction terms (platform × day(season) and platform × time(day)) identified as significant terms in the reef-dependent model were also significant factors of the reef-associated model. Although fewer samples were devoid of this functional group (48% for reef-associated vs. 65% for reef-dependent), the prevalent day-to-day variation in larval supply is still reflected in the platform × day(season) interaction term (Fig. 17). The final interaction term (platform × time(day) was also significant and reflects dawn to dusk differences among the platforms across all seasons (Fig. 18). The offshore platforms had greater amounts of reef-associated larval fishes collected during the dawn period, while the mid-shelf and coastal platforms had more larvae collected at dusk.

The reef-associated residuals were also not normally distributed (W:Normal = 0.95, $p < 0.001$), and examination of residual plots identified two potential outliers corresponding to summer and fall collections from GC18, where observed densities exceed the expected values by factors greater than four.

Catch composition of the reef-associated families collected during 1996 and 1997 is shown in Table 8. Three families (Lutjanidae, Carangidae, and Gobiidae) comprised 84.5% of the catch, with no other reef-associated family making up greater than 5% of this functional group. Length-frequency distributions for the lutjanids showed a much greater size range, as well as much higher numbers of individuals being

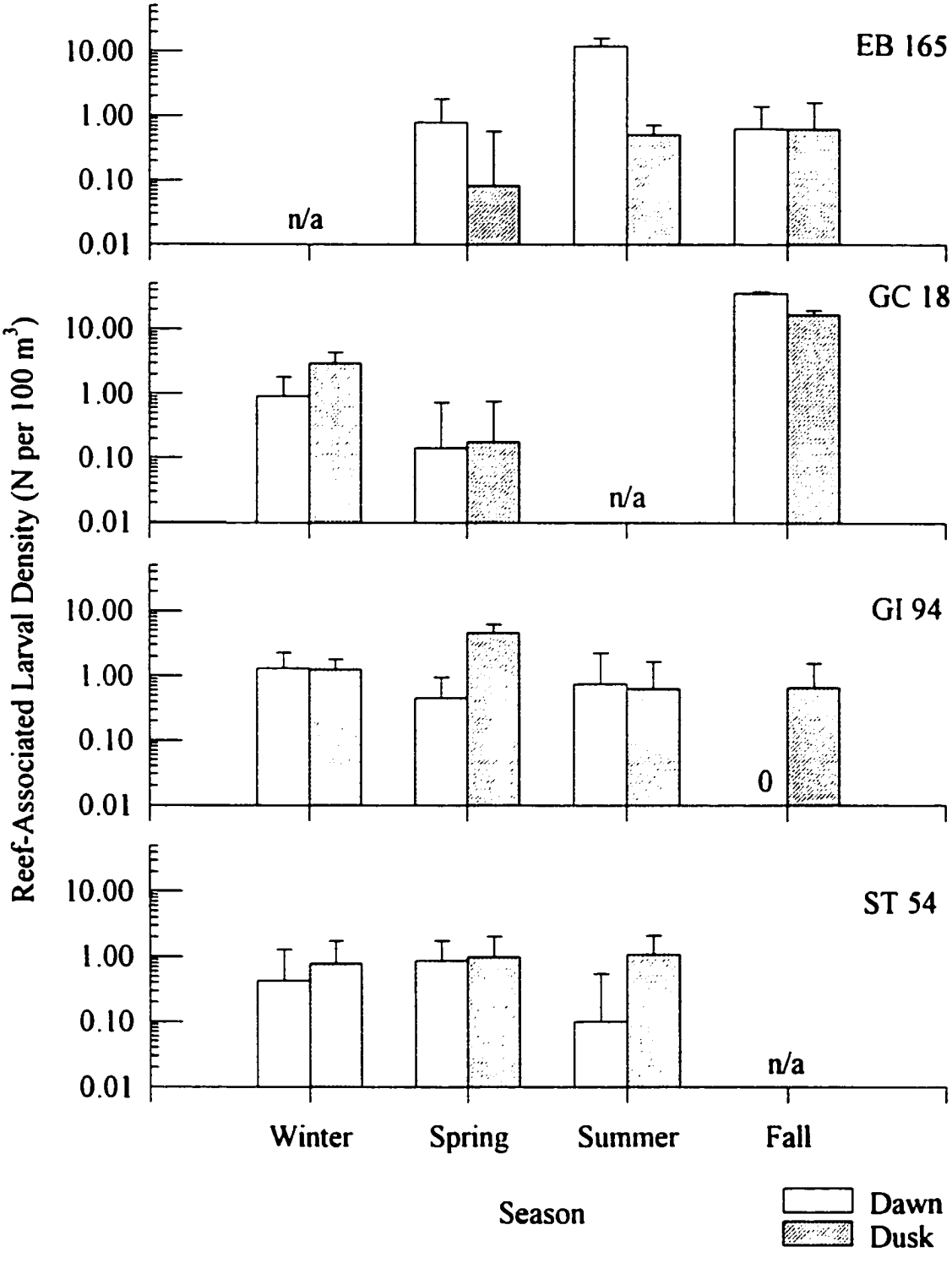


Figure 17. Mean density (Σ total number / 100 m^3; + SE) of the reef-associated functional group collected seasonally with the dawn-dusk sampling protocol from each study platform. N/A represents seasons not sampled; 0 represents seasons sampled but zero catch recorded.

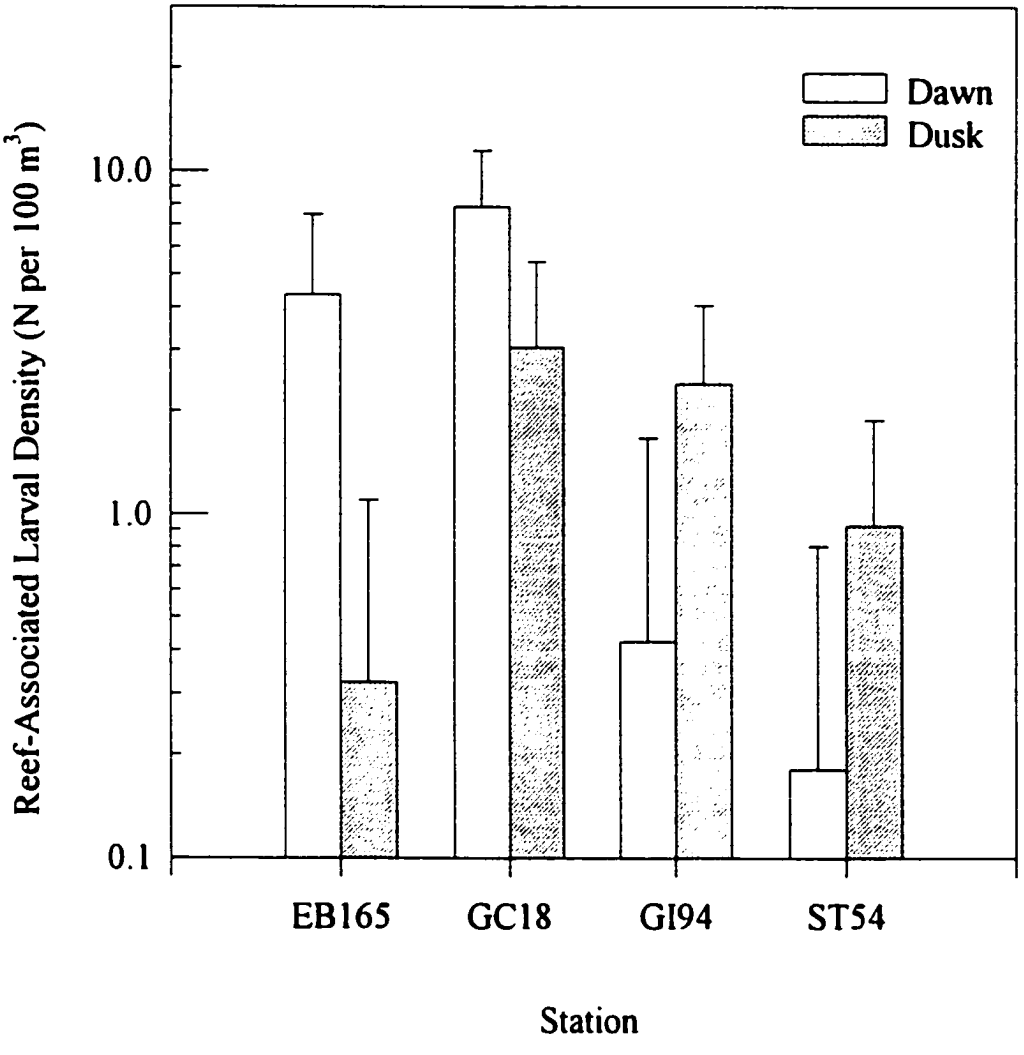


Figure 18. Mean density (Σ total number / 100 m^3; + SE) of the reef-associated functional group collected at dawn and dusk from each platform.

Table 8. Numbers of larvae from the reef-associated functional group, by family, collected at dawn and dusk from all platforms during 1996 and 1997. Percent Total = the contribution of each family to the total collection.

Family	Dawn	Dusk	Total	Percent Total
Lutjanidae	362	51	413	32.8
Carangidae	269	96	365	28.9
Gobiidae	100	187	287	22.8
Balistidae	55	5	60	4.8
Opistognathidae	0	45	45	3.6
Blenniidae	9	19	28	2.2
Mullidae	17	3	20	1.6
Priacanthidae	10	3	13	1.0
Gerreidae	9	2	11	0.9
Apogonidae	2	4	6	<0.5
Muraenidae	1	4	5	<0.5
Tetraodontidae	0	4	4	<0.5
Ephippidae	1	0	1	<0.1
Holocentridae	1	0	1	<0.1
Malacanthidae	1	0	1	<0.1

supplied to the offshore platforms (Fig. 19). More early-stage larvae, as well as greater numbers of late-stage individuals, were collected from the eastern-most GC18 (GC18 median = 3.8 mm SL, SD = 1.18; EB165 median = 2.9 mm SL, SD = 0.49; $\chi^2 = 33.94$, N = 213, df = 7, $p < 0.001$). The supply pattern of carangid larvae to the mid-shelf and offshore platforms was similar to the carangids (Fig. 20). Disregarding the largest individuals (> 11 mm SL or size range of individuals typically caught in association with *Sargassum* or other flotsam that entered the net), more early-stage larvae were collected at GC18 than EB165 (median = 3.2 mm, SD = 1.17 vs. median = 3.5 mm, SD = 1.13, respectively). Similar size carangids were collected at GI94 (median = 3.6 mm SL, SD = 0.99). Chi-square tests showed the length-frequency distributions across platforms was significantly different ($\chi^2 = 62.04$, N = 497, df = 18, $p < 0.001$) although the comparisons involving GI94 had a lower N by a factor of > 4. The coastal platform (ST54) had the lowest supply of Carangidae larvae, and the larvae had a nearly uniform length-frequency distribution ranging from 4 to 12 mm (median = 7.1 mm SL, S.D = 2.2).

Gobiids differed from the other dominant reef-associated families in that the abundance of early larvae (3 to 5 mm SL) was more equally distributed among the mid-shelf and offshore platforms (Fig. 21). Length-frequency distributions of Gobiidae larvae from GI94 (median = 5.0 mm SL, SD = 1.54) were similar to those collected at both GC18 (median = 5.7 mm SL, SD = 1.57) and EB165 (median = 4.9 mm SL, SD =1.15), although GC18 had significantly larger larvae from EB165 ($\chi^2 = 98.78$, N =

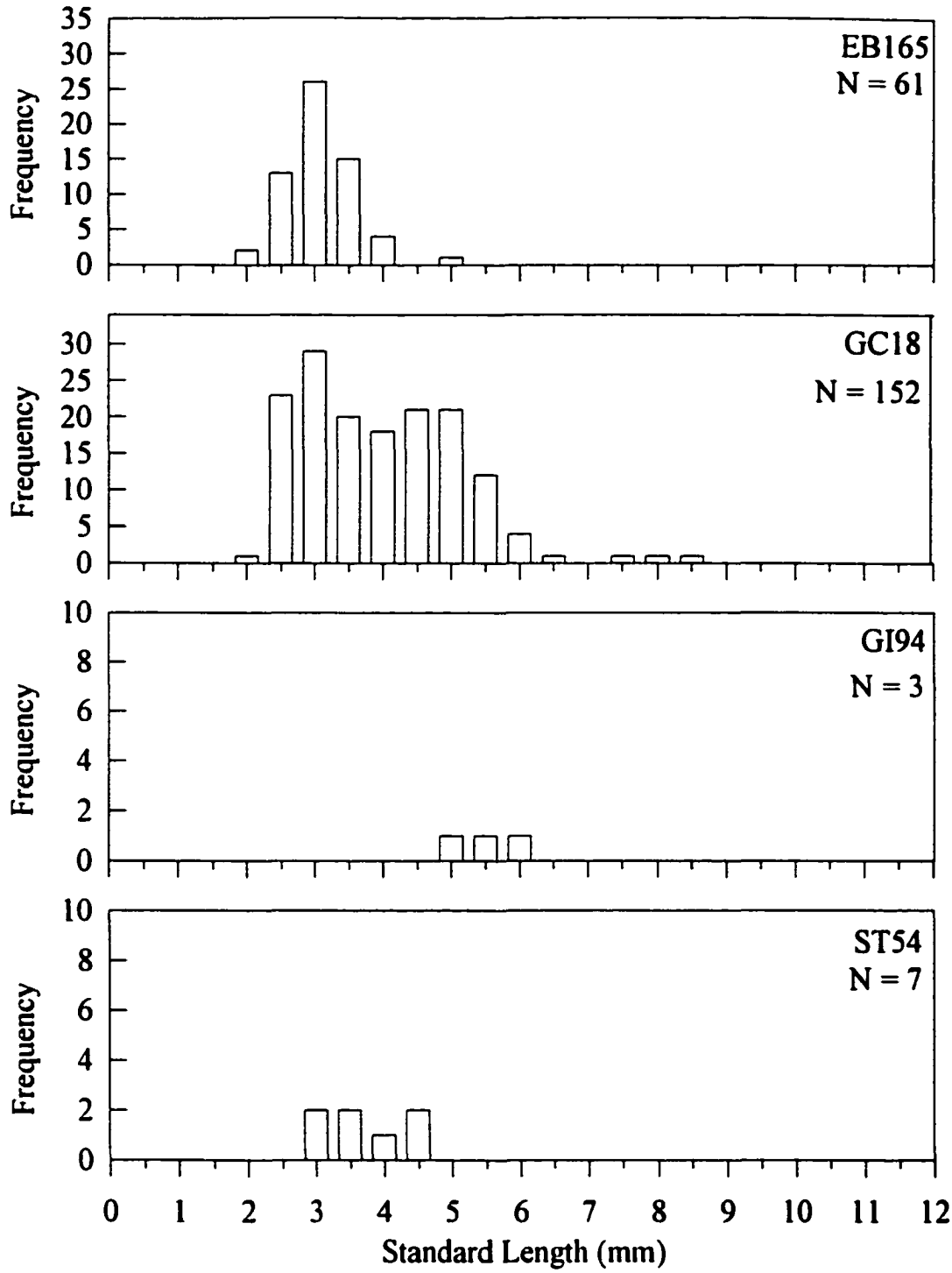


Figure 19. Length-frequency distributions (SL) of Lutjanidae larvae collected from each platform (all years 1994 -1997). Note change in the *y*-axis between the offshore stations (EB165 and GC18) and the near-shore stations (GI94 and ST54). N = total number of individuals measured.

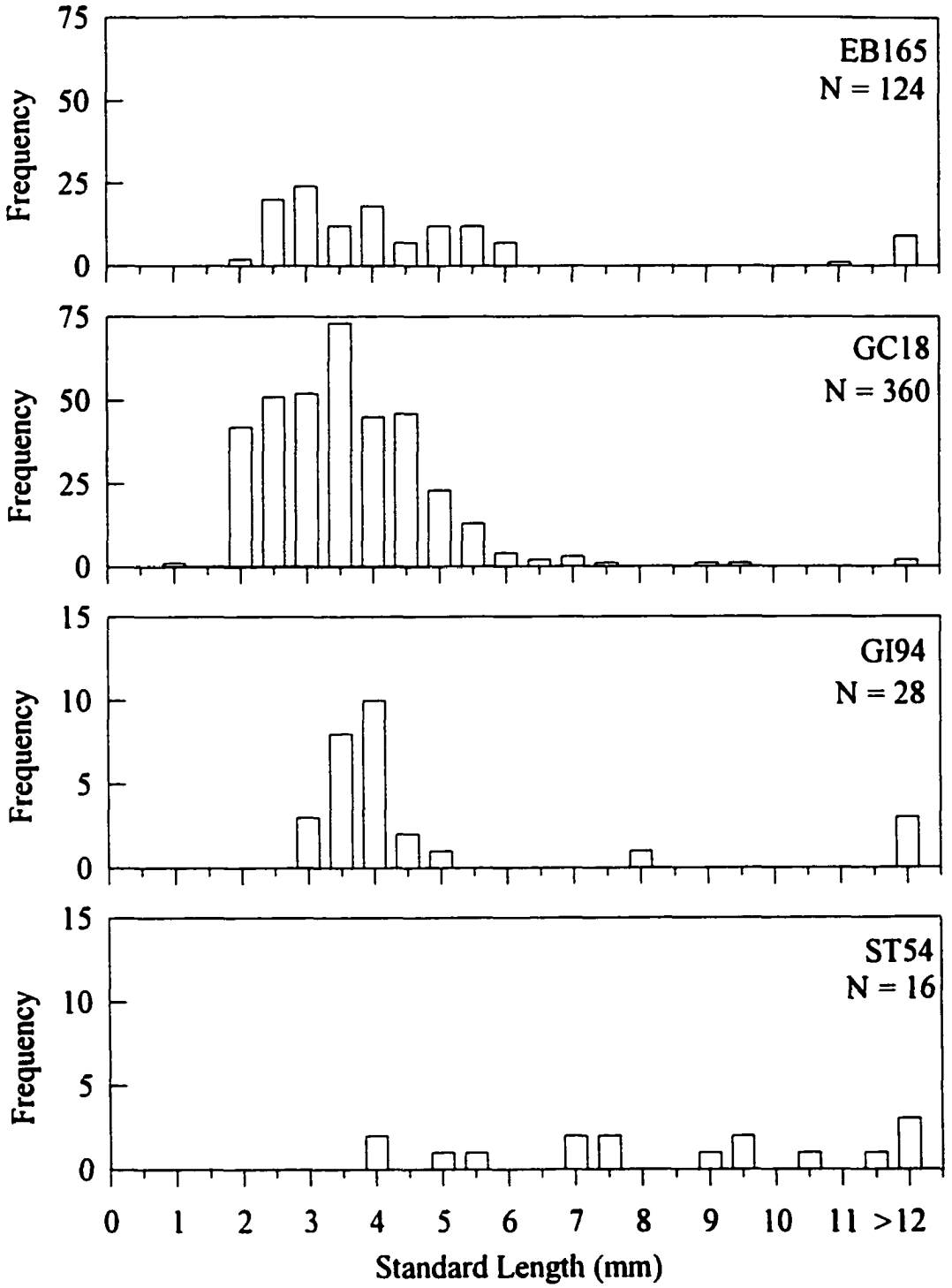


Figure 20. Length-frequency distributions (SL) of Carangidae larvae collected from each platform (all years 1994 - 1997). Note change in the *y*-axis between the offshore stations (EB165 and GC18) and the near-shore stations (GI94 and ST54). N = total number of individuals measured.

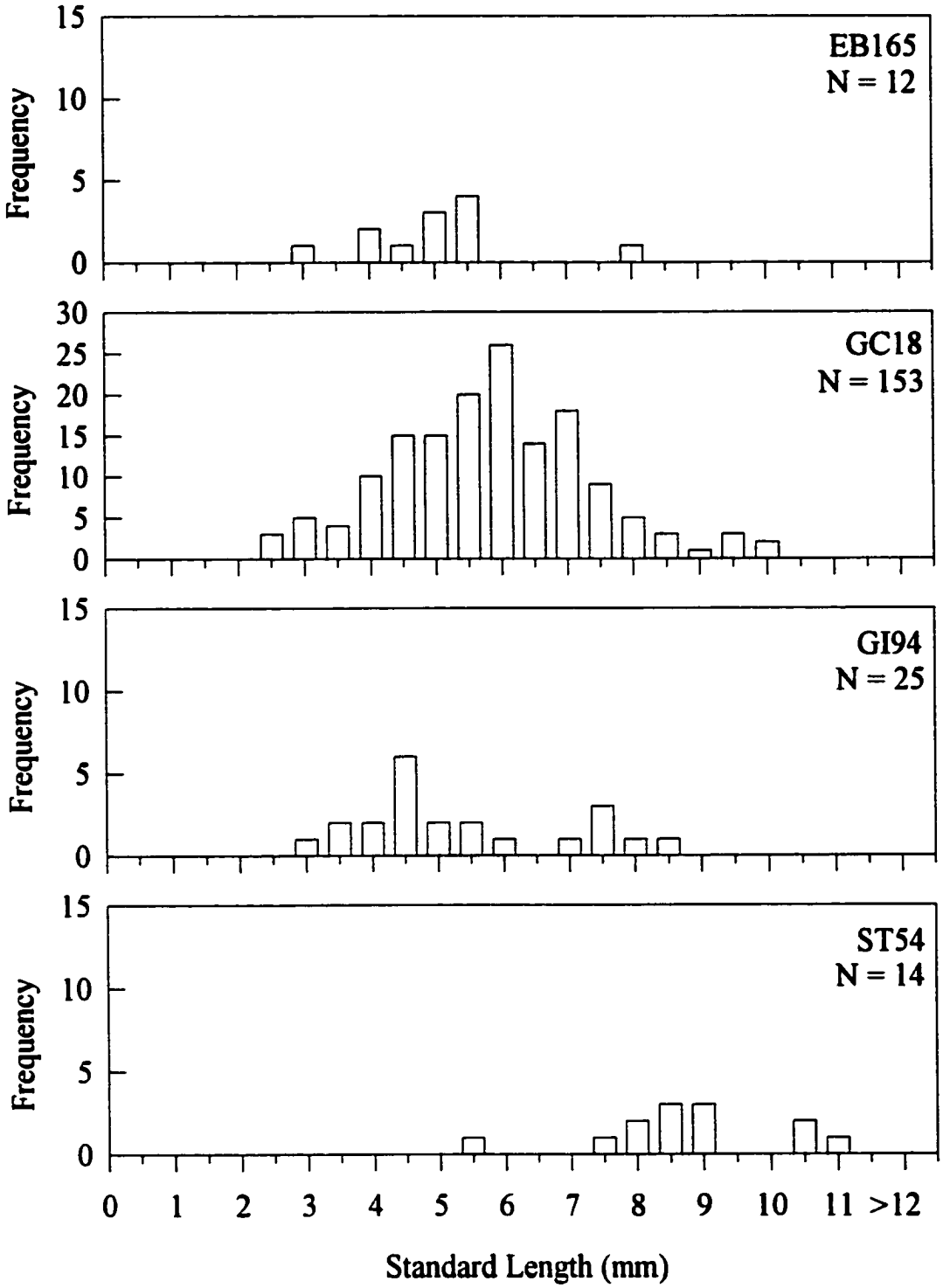


Figure 21. Length-frequency distributions (SL) of Gobiidae larvae collected from each platform (all years 1994 - 1997). Note change in the *y*-axis between GC18 and all other platforms. N = total number of individuals measured.

204, df = 27, $p < 0.001$). Because the size range of gobiid larvae collected from ST54 was dominated by the 8 to 9 mm SL size class, the coastal platform was identified as significantly different from all other platforms.

Light Aggregation Devices

1994 and 1995 – Light Traps

Mean CPUE for total ichthyoplankton between the surface and deep light traps did not differ significantly (unequal variance $t = 1.71$, $p = 0.10$), although both catch rates were far lower than the surface plankton net (surface LT = 0.1 fish / hour, SD = 0.34; deep LT = 0.6 fish / hour, SD = 0.96). Light trap collections were then pooled (surface and -20 m depth) and compared to the pooled surface net collections taken at the same times (pooled dusk and midnight catches). The surface nets caught significantly more total larvae (pooled plankton nets = 49.5 fish / hour, SD = 33.89; pooled light traps = 0.3 fish / hour, SD = 0.75), exceeding the light trap average CPUE by two orders of magnitude (unequal variance $t = 8.23$; df = 22.02; $p < 0.001$).

1996 and 1997 – Lighted vs. Unlighted Plankton Nets

Mean density of the total ichthyoplankton collected with the lighted plankton nets differed significantly among the three platforms during the summer ($F_{(2, 35)} = 13.31$; $p < 0.001$), although no significant differences between the lighted and unlighted method could be detected. Seasonal total ichthyoplankton was highest farther offshore at dusk, followed by the nearshore coastal area (Fig. 22). Significantly lower total density was recorded from the mid-shelf area at GI94.

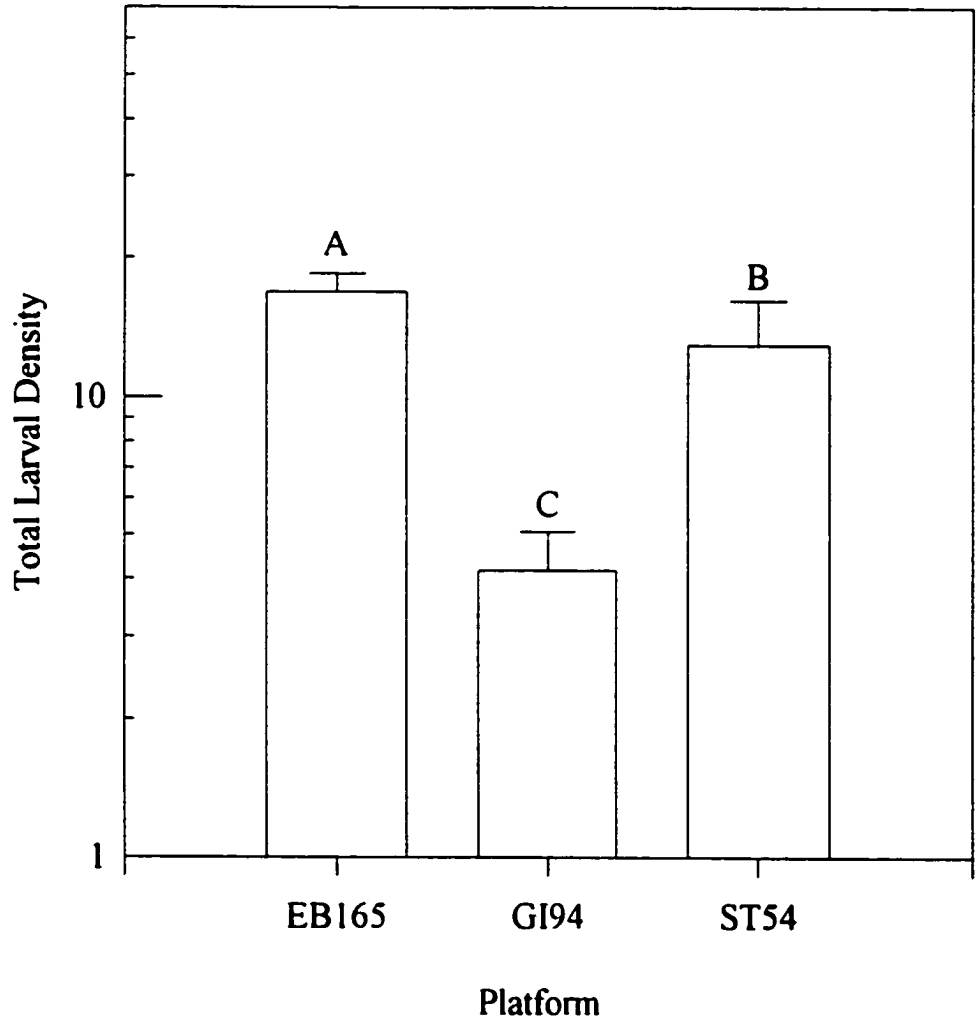


Figure 22. Mean density (Σ total number / 100 m^3; + SE) of surface ichthyoplankton collected with the lighted plankton net gear during the summer seasons of 1996 and 1997. Letters indicate the results of the REGWQ test where means with the same letter are not significantly different.

Seasonal comparisons (spring, summer, and fall only) of the total ichthyoplankton collected at GI94 alone showed significant differences in the amount of supply by season ($F_{(2, 45)} = 19.2$; $p < 0.001$) yet no differences were noted between the lighted and unlighted collections. Although the spring season had significantly higher densities of total ichthyoplankton in the surface waters (Fig. 23), no light main effect differences were seen in the catch rates between the lighted and unlighted passive nets ($F_{(1, 45)} = 2.05$; $p = 0.16$, lighted mean = 8.7 individuals / 100 m^3, SD = 7.99; unlighted mean = 8.1 / 100 m^3, SD = 6.36).

Residual analysis of the total ichthyoplankton supply showed that while neither platform nor seasonal comparisons violated the normal distribution assumptions, neither ANOVA explained greater than 50% of the total variation seen (platform comparisons $R^2 = 0.44$; C.V. = 36.6, seasonal comparisons $R^2 = 0.47$; C.V. = 32.6). Power analysis showed that more than enough samples were collected to adequately detect both platform and seasonal differences (see Appendices B.4.a and B.4.b).

Lighted vs. Unlighted Nets: Reef-Dependent Functional Group

Most samples contained no larvae from the reef-dependent functional group. The platform comparison analysis of reef-dependent density could not be performed because no larvae were collected during the summer collections from any of the three platforms. Of the 41 samples that comprised the seasonal analysis of GI94, only six samples (or 14.6%) contained any larval reef-dependent families. Densities were higher with the unlighted net (unlighted mean = 0.9 individuals / 100 m^3, SD = 1.94; lighted

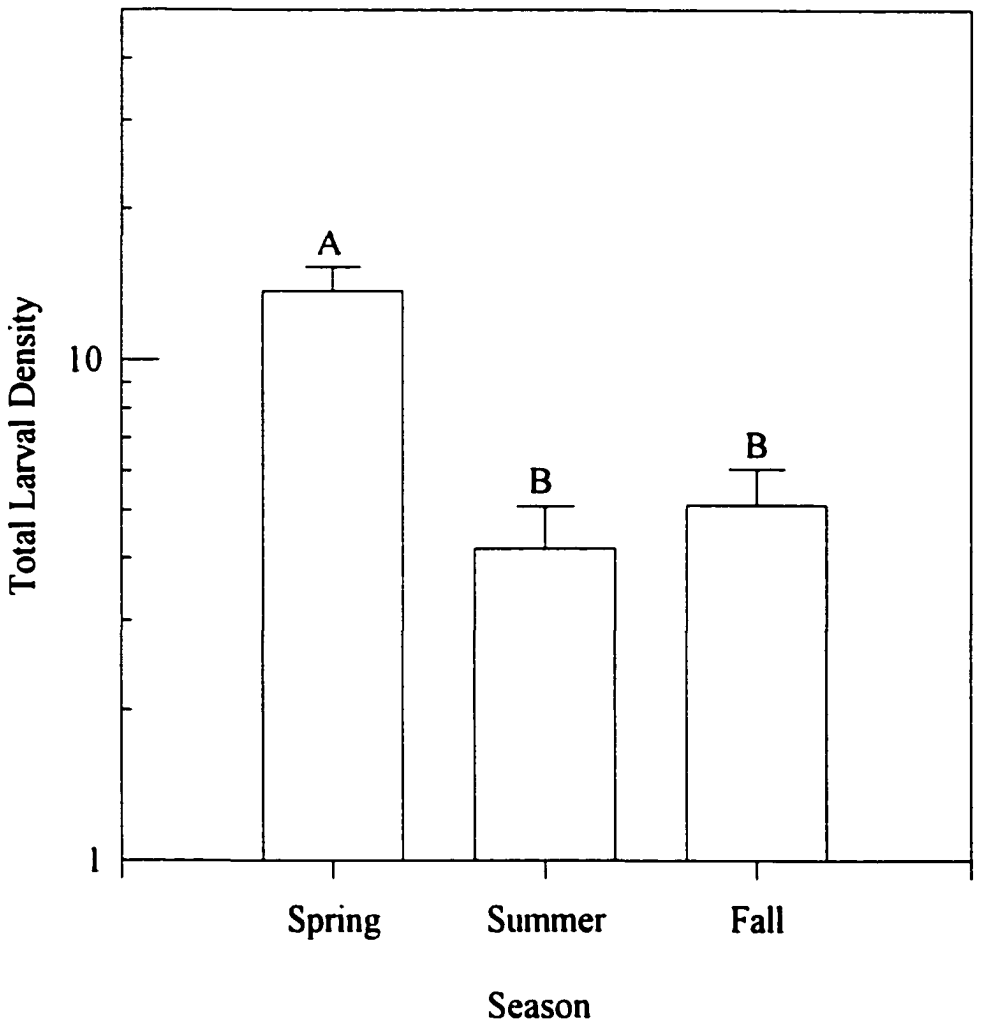


Figure 23. Mean density (Σ total number / 100 m^3; + SE) of surface ichthyoplankton collected seasonally (spring, summer, and fall) with the lighted plankton net gear at GI94 during 1996. Letters indicate the results of the REGWQ test where means with the same letter are not significantly different.

mean = 0.1 / 100 m^3, SD = 0.28). No significant differences among either main effects nor their interactions were detected. Residuals were not normally distributed (W:Normal = 0.79, $p < 0.001$), reflective of the numerous zeros comprising the reef-dependent lighted plankton net data set. This general lack of fit with the two-way ANOVA was reflected in a high coefficient of variation (C.V. = 236.65) and low overall model R^2 (0.28).

Lighted vs. Unlighted Nets: Reef-Associated Functional Group

The density of reef-associated larvae was also low at each platform during summer, although there was a smaller percentage of zeros overall with this functional group (56.1% for reef-associated vs. 84.6% for reef-dependent). Mean density was significantly different among the three platforms ($F_{(2, 45)} = 3.50$; $p = 0.04$; see Fig. 24), although there were no differences between the light main effect nor the platform × light interaction. Highest densities were recorded at the nearshore platform (mean = 1.2 individuals / 100 m^3, SD = 0.96), where carangids and gobiids made up the largest portion of the catch. The mid-shelf and offshore platforms received less than half this amount of reef- associated supply during the summer season.

The two-way ANOVA again explained only a small portion of the total sums of squares ($R^2 = 0.18$), with the platform main effect accounting for nearly all this amount (90.2%). Examination of the residuals (W:Normal = 0.91, $p = 0.002$) revealed a single potential outlier, corresponding to an unusually high catch with the lighted net from EB165 during summer of 1997 (mean density = 4.4 individuals / 100 m^3, studentized residual = 3.56).

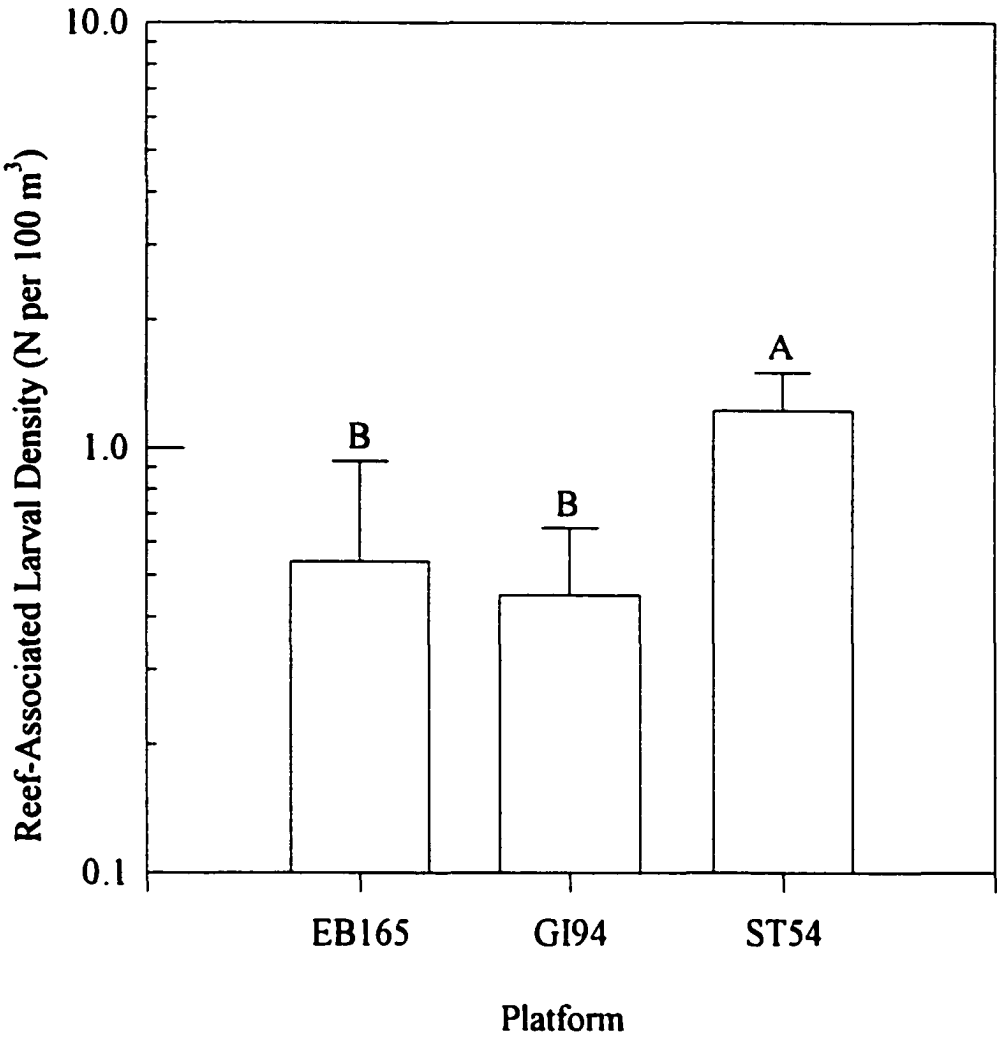


Figure 24. Mean density (Σ total number / 100 m^3; + SE) of the reef-associated functional group collected with the lighted plankton net gear during the summer seasons 1996 and 1997. Letters indicate the results of the REGWQ test where means with the same letter are not significantly different.

While the densities of reef-associated families fluctuated seasonally at GI94 ($F_{(2, 44)} = 7.57$; $p < 0.01$; Fig. 25), no differences between the lighted and unlighted nets were found ($F_{(1, 44)} = 0.07$; $p = 0.80$), although with the effect size seen between the lighted and unlighted nets, 1,982 samples would have been needed in order to show significant differences in the light main effect (Appendix B.7). Seasonal differences accounted for 93.2% of the model sum of squares, which reflected only a small portion of the total ($R^2 = 0.270$).

Lighted vs. Unlighted Nets: Length-Frequency Analysis

The total ichthyoplankton catch from the lighted plankton net deployments (N = 7,562 individuals) listed by family is shown in Table 9 (with total number per family representing only those individuals measured for analysis, which in many cases was a subsample of a much larger catch). Most families were equally represented in the lighted and unlighted nets (% total lighted net ranged between 45 and 65%). Some families however, displayed negative phototaxic responses (i.e., Scombridae, Gonostomatidae, and Myctophidae). These families were all collected in lower densities with the light-aggregating device. Only the sciaenid and synodontids showed strongly positive phototaxis.

The only family to show a significant interaction between collection method and study platform was the gonostomatids (Table 10), with an increased proportion of larvae collected with the lighted net at EB165. Similar proportions of gonostomatids were collected by each gear from the mid-shelf platform and they were absent from the

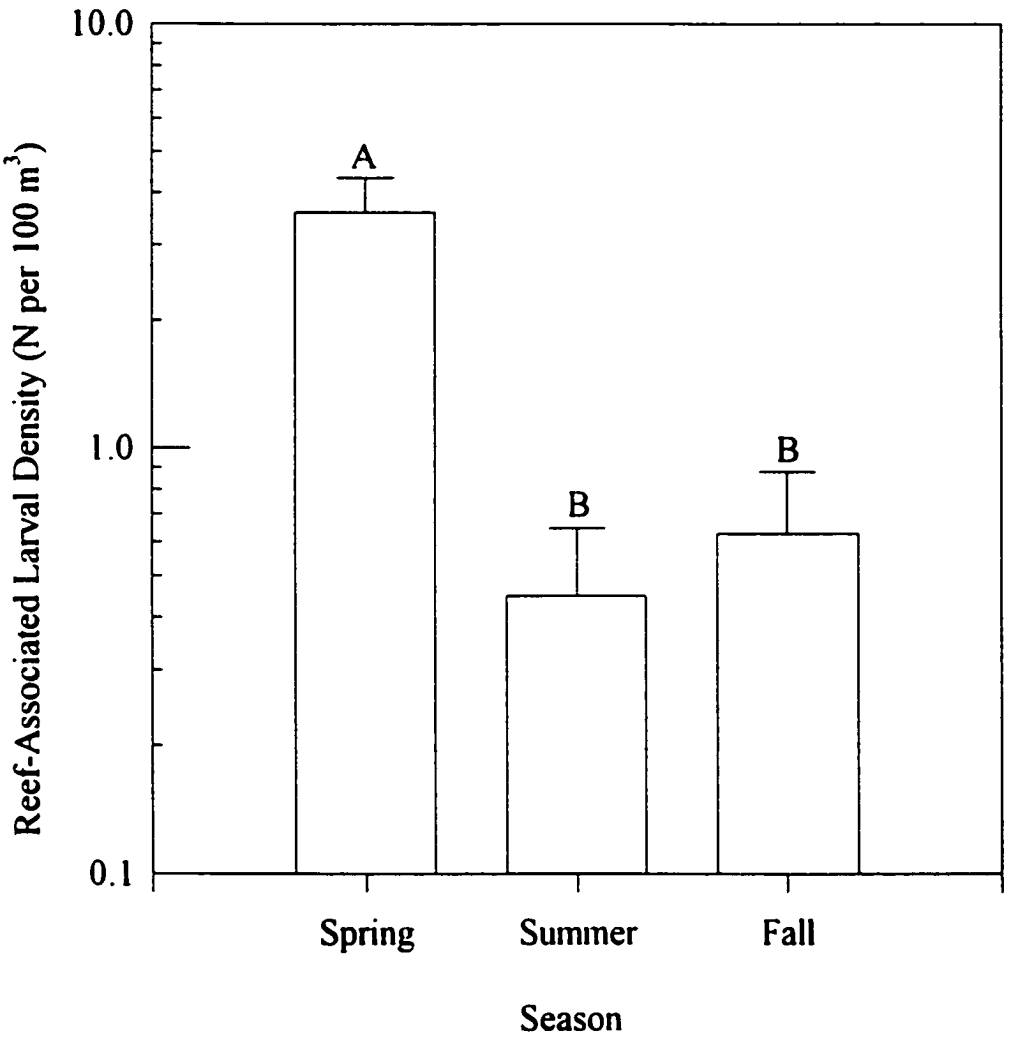


Figure 25. Mean density (Σ total number / 100 m^3; + SE) of the reef-associated functional group collected seasonally (spring, summer, and fall) with the lighted plankton net gear at GI94 during 1996. Letters indicate the results of the REGWQ test where means with the same letter are not significantly different.

Table 9. Numbers of larvae of all other families (not including reef functional groups) collected with the surface nets (lighted and unlighted) from all platforms combined during 1996 and 1997. % Total LPN = percent total from lighted deployments.

Family	Unlighted	Lighted	Total	% Total LPN
Clupeiformes	187	192	379	50.7
Cynoglossidae	52	72	124	58.1
Scombridae	79	16	95	16.8
Bothidae	26	37	63	58.7
Sciaenidae	19	39	58	67.2
Synodontidae	11	21	32	65.6
Mugilidae	13	18	31	58.1
Bregmacerotidae	15	15	30	50.0
Gonostomatidae	19	2	21	9.5
Myctophidae	11	4	15	26.7
Soleidae	5	10	15	66.7
Triglidae	7	2	9	22.2
Hemiramphidae	3	2	5	40.0
Ophichthidae	3	1	4	25.0
Ophidiidae	1	3	4	75.0
Exocoetidae	3	0	3	0.0
Congridae	1	1	2	50.0
Sphyraenidae	1	1	2	50.0
Centriscidae	0	1	1	100.0
Coryphaenidae	0	1	1	100.0
Istiophoridae	1	0	1	0.0
Syngnathidae	0	1	1	100.0
Trichiuridae	1	0	1	0.0

Table 10. Density of nine most-abundant taxa from the Lighted Plankton Net collections during 1996 and 1997. Chi-square test statistic for platform × light test of independence (NS; not significant at $\alpha = 0.05$). Numbers in parenthesis = % of total collection in each gear type.

Taxa	Platform			χ^2	p
	ST 54	GI 94	EB 165		
Clupeiformes					
Lighted	1715.6 (49.9 %)	229.4 (50.5 %)	5.5 (100 %)	5.01	0.08 (NS)
Unlighted	1720.2 (50.1 %)	224.5 (49.5 %)	0.0 (0 %)		
Cynoglossidae					
Lighted	36.2 (50.9 %)	0.8 (0.2 %)	0.0	1.76	0.18 (NS)
Unlighted	34.8 (49.1 %)	3.6 (98.8 %)	0.0		
Scombridae					
Lighted	0.0	13.9 (25.1 %)	13.2 (30.1 %)	0.26	0.61 (NS)
Unlighted	0.0	41.5 (74.9 %)	30.7 (69.9 %)		
Bothidae					
Lighted	0.0 (0%)	9.3 (49.5 %)	13.6 (51.7 %)	1.04	0.60 (NS)
Unlighted	0.5 (100 %)	9.5 (50.5 %)	12.7 (48.3 %)		
Sciaenidae					
Lighted	17.9 (57.7 %)	6.2 (57.9 %)	4.4 (100 %)	2.86	0.24 (NS)
Unlighted	13.1 (42.3 %)	4.5 (42.1 %)	0.0 (0 %)		
Synodontidae					
Lighted	0.5 (45.5 %)	33.9 (67.8 %)	0.0	0.24	0.63 (NS)
Unlighted	0.6 (54.5 %)	16.6 (32.2 %)	0.0		
Mugilidae					
Lighted	0.0	19.7 (42.5 %)	0.0	N/A	
Unlighted	0.0	26.6 (57.5 %)	0.0		
Bregmacerotidae					
Lighted	0.0	19.8 (47.7 %)	0.0	N/A	
Unlighted	0.0	21.7 (52.3 %)	0.0		
Gonostomatidae					
Lighted	0.0	3.6 (57.1 %)	0.0 (0 %)	5.60	0.02 *
Unlighted	0.0	2.7 (42.9 %)	6.8 (100 %)		

coastal platform. Of the eight other most abundant families, each maintained consistent collection patterns across platforms (no difference between methods – Clupeiformes, Cynoglossidae, Bothidae, Mugilidae, and Bregmacerotidae; positive phototaxis – Sciaenidae and Synodontidae; and negative phototaxis – Scombridae).

The three most abundant families were investigated with Chi-square tests to determine if their length-frequency distributions were similar for both nets (Fig. 26). The Clupeiformes were numerically abundant in both nets, although the lighted net caught greater numbers of larger sized individuals ($\chi^2 = 24.99$, N = 379, df = 17, p = 0.09). The cynoglossids' were caught at a larger median size than most other abundant ichthyoplankton (cynoglossid median = 10.8 mm SL, SD = 0.95 vs. overall lighted plankton net median = 5.9 mm SL, SD = 3.81), with substantially more individuals being collected with the lighted net at the near-shore station. The shapes of the two distributions for the cynoglossids were significantly different ($\chi^2 = 18.12$, N = 124, df = 7, $p = 0.01$). Scombrids displayed a negative phototaxic response, with only 16.8 % of the total catch coming from the lighted net, and were caught primarily at EB165 (although the largest individuals (> 7.0 mm SL) all came from the mid-shelf platform). Their length-frequency distributions were not significantly different between the two gears ($\chi^2 = 14.74$, N = 95, df = 8, $p = 0.06$).

Numerically abundant larval fishes from the reef-associated functional group were also investigated with the Chi-square procedure, and no differences between their size distributions could be found (Fig. 27). In each case, the sample sizes are low and the distributions not well defined.

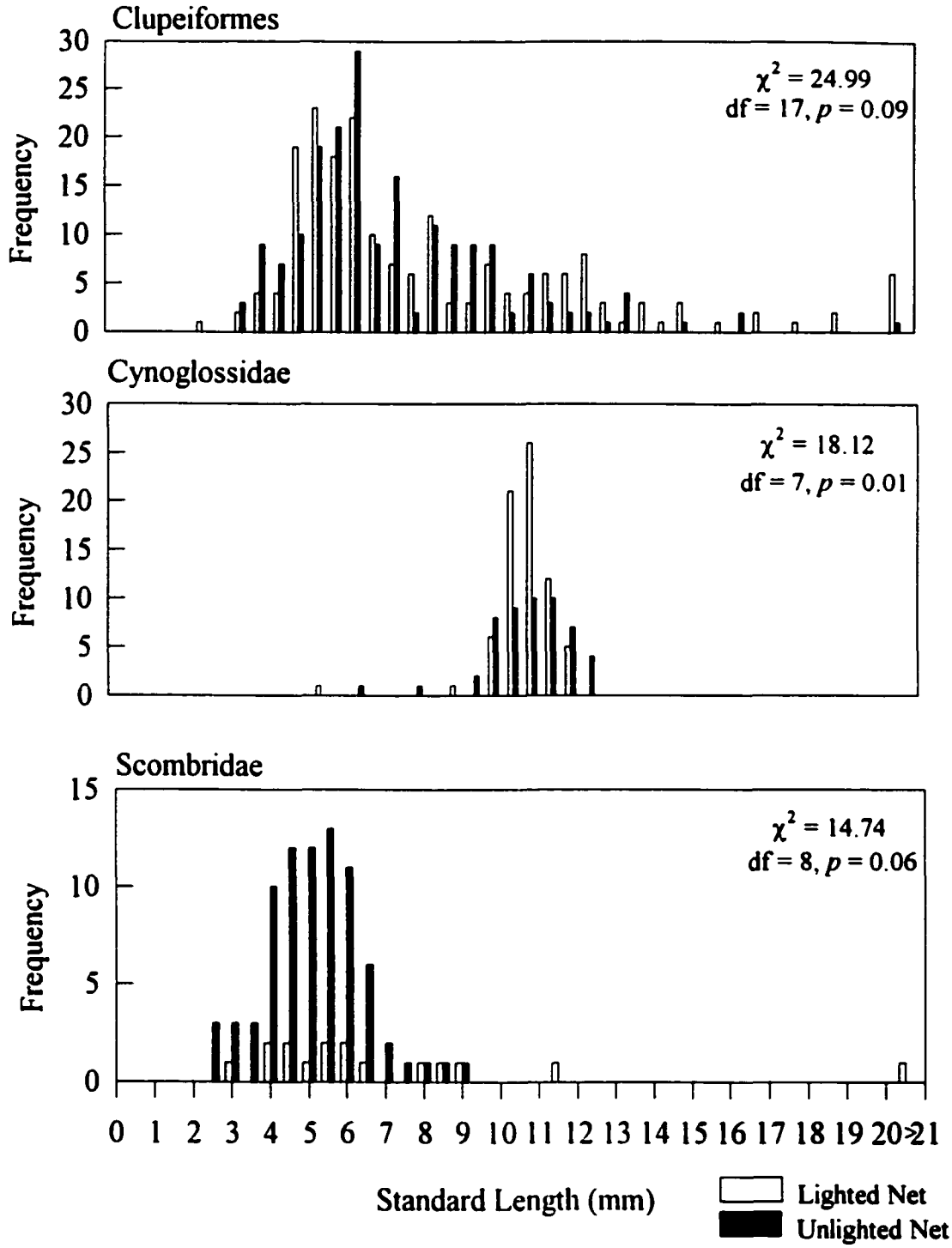


Figure 26. Length-frequency distribution comparisons (Chi-square test) of numerically abundant larvae collected with the lighted plankton net gear from EB165, GI94, and ST54 during 1996 and 1997.

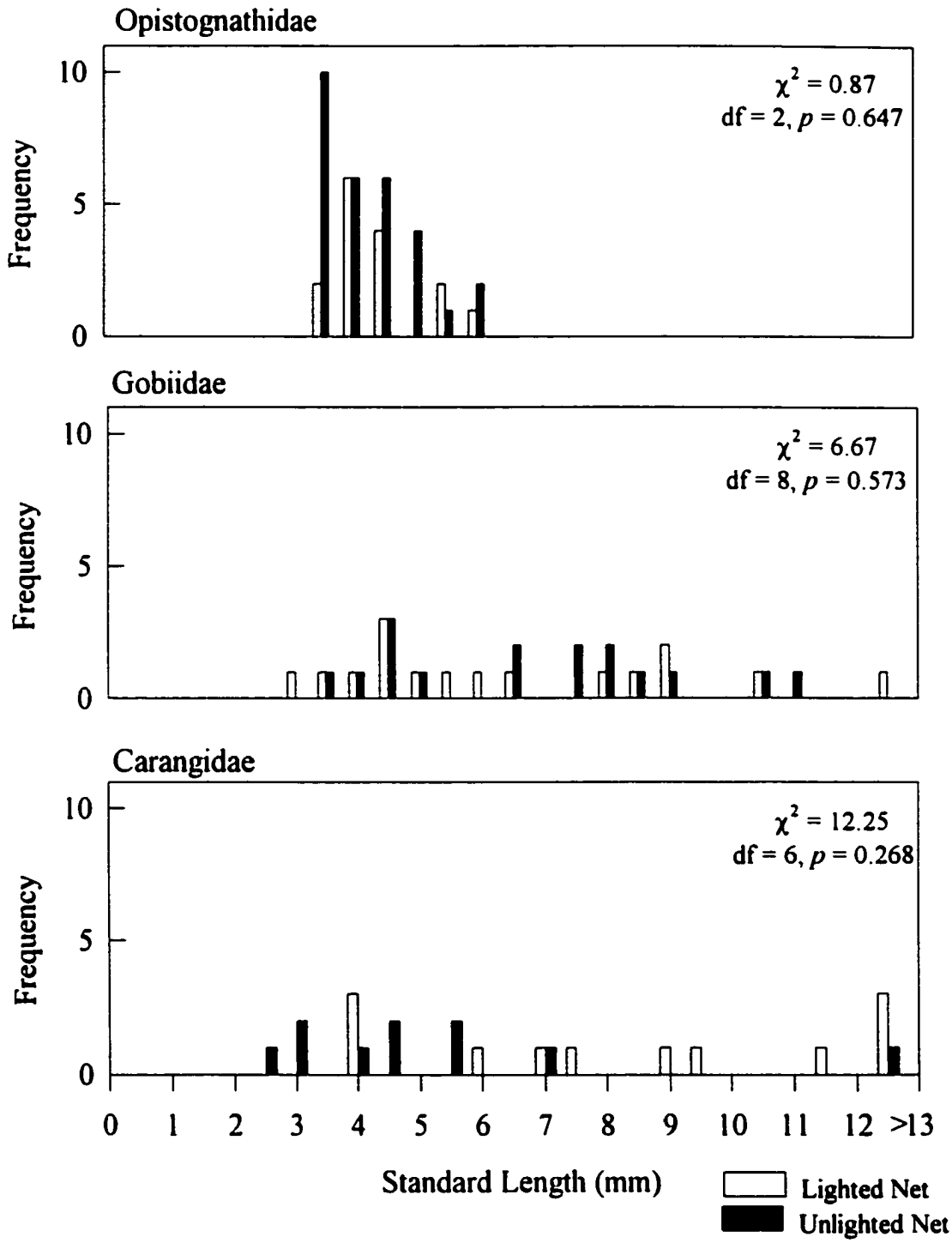


Figure 27. Length-frequency distribution comparisons (Chi-square test) of numerically abundant reef-associated larvae collected with the lighted plankton net gear at EB165, GI94, and ST54 during 1996 and 1997.

Discussion

The supply of larvae to potential juvenile habitats is an important factor in determining the distribution, abundance, and year-class strength of many marine species (Milicich et al. 1992; Doherty and Fowler 1994b, Stoner et al. 1997). Surveys of ichthyoplankton assemblages help to identify not only spawning areas, times, and the size of larval populations (Victor 1983; Richards et al. 1993), but they also provide an indirect measure of planktonic movement via transport in oceanic currents (Tolimieri et al. 1998). Because recruitment to artificial reef habitats is thought to occur primarily by larval settlement out of the plankton (and secondarily, through colonization by older juveniles and adults in near-shore areas; see Bohnsack et al. 1994), ichthyoplankton supply to each platform was viewed as a potential source of recruitment.

Family-level taxonomic richness of the ichthyoplankton reported in this study (80 families) is similar to previously reported surveys: 1) in the northern Gulf above 26°00'N (61 families, Ditty et al. 1988); 2) from offshore waters of the entire northern Gulf (74 families, Richards et al. 1984); 3) from collections near coral reefs in the northwestern Gulf (85 families, McGowan 1985); and 4) from sampling from near the Florida Keys (91 and 100 families, Limouzy-Paris et al. 1994 and Richards et al. 1993, respectively). The rank order of the 10 most abundant families collected during this study (in terms of total numbers), compared to 6 other ichthyoplankton studies from the Gulf (Finucane 1976, Finucane et al. 1977, Houde et al. 1979, McGowan 1985, Kelley et al. 1986, Limouzy-Paris et al. 1994) are presented in Table 11.

Table 11. Rank order comparison of the 10 most abundant families of larval fishes collected during ichthyoplankton surveys of the Gulf of Mexico (Clupeidae and Engraulidae combined and listed as Clupeiformes). Rank is based on the total number of individuals collected. * Families identified for this study as either reef-dependent (RD) or reef-associated (RA).

Taxa	Present Study	Finucane 1976	Finucane et al. 1977	Houde et al. 1979	McGowan 1985	Kelley et al. 1988	Limouzy-Paris et al. 1994
Clupeiformes	1	1	2	1	9	1	8
Myctophidae	2	8	5	5	5	2	2
Carangidae *RA	3	5	7	7		6	9
Lutjanidae *RA	4						
Scombridae	5		9				7
Serranidae *RD	6	9		6	10		6
Mugilidae	7					9	
Gobiidae *RA	8	2	1	2	1	3	3
Cynoglossidae	9				8		
Ophidiidae	10						
Bothidae		6	4	4	3	5	5
Bregmacerotidae		3	3	3	2	4	1
Sciaenidae		4	8			8	
Synodontidae		7	6	8	4		
Labridae *RD				9			
Gonostomatidae				10	7	7	4
Anguilliformes					6		

Although most other ichthyoplankton surveys incorporated some form of depth-integrated sampling (MOCNESS, obliquely towed nets, etc.) with catches typically reported in terms of abundance (N under per unit m^2 area of sea surface), the family richness reported from this surface water survey adequately documents the family-level larval richness found in the Gulf. Clupeiformes numerically dominated this, as well as four of the other six ichthyoplankton surveys (rank order = 1 or 2, see Table 11). Reef fish that ranked high in this study (e.g., Carangidae and Serranidae) are also noted as ranking high from other surveys. Reef fish families that ranked substantially differently included the gobiids (8^{th} most abundant from this study vs. one of the top three from each of the other studies) and the lutjanids (4^{th} most abundant from this study vs. not listed from the six other surveys). As with many other ichthyoplankton surveys, most reef fish families (both reef-dependent and reef-associated) are not routinely encountered in the plankton.

Ichthyoplankton family-level richness at GC18 during 1994 and 1995 showed a marked seasonality, although the pattern was concomitant with diurnal periodicity. Overall, richness was evenly distributed between the sampling periods during winter and spring, with higher richness values recorded at dawn and noon during the summer (Fig. 7). Both the dusk and midnight periods showed seasonal increases reaching maximum values in the fall, whereas the richness values for dawn and noon sample times exhibited minimum fall values. Diurnal periodicity can effect the richness levels of fishes found in surface waters, because larvae of many fishes have been shown to actively migrate on a diurnal basis. These planktonic larvae tend to move upward in

the water column in the late afternoon/early evening, move downward during the middle of the night, move upward again just before sunrise, and then descend again to a preferred daytime depth (Leis 1991c). Family-level richness values from GC18 during 1994 and 1995 appears to be following this general pattern (e.g., higher family-level richness during the dawn and dusk periods).

In a two-year study of the ichthyoplankton near the Flower Garden Banks (located on the shelf-break near EB165), McGowan (1985) also noted maximal family-level richness and abundance during the autumn months, which was attributed primarily to the hydrography of the study area. The seasonal thermocline, which is not well pronounced in the winter, is fairly shallow in the spring (20-30 m) and deepens with the stronger thermal energy input during summer (down to 40-50 m). Fall stratification persists, with the thermocline reaching its maximum depth of 50-60 m (McGrail et al. 1982), until cold frontal passages mix the upper water column over the continental shelf. Maximal values of larval richness coincided with this large, stable water mass (summer and fall seasons).

Diurnal periodicity in the densities of both functional groups (reef-dependent and reef-associated) were also evident at GC18 during 1994 and 1995. Overall, densities of both groups were seasonally highest during summer. For reef-dependent larvae, the dawn sampling time was the period of highest densities in winter, spring, and summer (Fig. 11), and this dawn dominance was seasonally similar to the reef-associated group during winter and spring (Fig. 12). Maximum densities of both functional groups were recorded during the noon sample time during summer, although

the densities of the reef-associated functional group were over an order of magnitude higher than the reef-dependent group. Densities of each group were typically low during the midnight sample time regardless of season.

For each reef fish functional group, the temporal patterns of larval supply identified at GC18 alone were assessed for greater spatial consistency with ichthyoplankton sampling from the four study locations in 1996 and 1997. Much of the seasonal variation that was identified was due, in part, to the physical location of each platform. The supply of reef-dependent families to the shelf-break and mid-shelf platforms was greatest in the spring, whereas the near-shore platform had highest reef-dependent supply during winter (Fig. 12). Serranids accounted for the majority of the reef-dependent individuals collected, and this disparity between onshore-offshore seasonal peaks may be the result of combining numerous species at the family level. Reef-associated families also showed a disparity in seasonal peaks in supply, with the near-shore and mid-shelf platforms having maximum densities in spring whereas the shelf-break platforms experienced spring minimums (Fig. 17). Again, mixtures of species within the various reef-associated families could also help explain these seasonal differences.

Despite being collected at such low densities, peak seasonal occurrences for many families identified during this study (Serranidae, spring and fall; Carangidae, spring and summer; and Lutjanidae, spring) all agree well with peak occurrences of larval fishes for the northern Gulf (Ditty et al. 1988). These patterns also reinforce the findings of Munro et al. (1973), where maximal spawning for 83 species of shallow-

water reef fishes on the southern coast of Jamaica was recorded during periods of minimal water temperatures (< 28 °C, or February, March, and April). McGowan (1985) showed an additional early autumn peak for some reef fishes around the Flower Gardens (lutjanids, gerreids, scarids, balistids), which he attributed to increased survival due to favorable currents patterns rather than a peak in spawning. The density levels of larval reef fish families reported by McGowan (1985) near a hermatypic reef complex were quite similar to the density levels I found on artificial reefs 30 to 180 km away (EB165 and GC18, respectively).

When present in the surface waters, highest densities (ranging from 1.0 to 10's of larvae / 100 m^3 of water) of each functional group were typically found at the deeper, shelf-break platforms. Onshore-offshore gradients in the abundance of larval reef fish have been documented for tropical islands (Leis 1986; Lobel and Robinson 1986; Boehlert et al. 1992), where many families that spawn via pelagic eggs show highest concentrations away from any reef source (at scales of 5 to 50 km). The larvae of the most conspicuous reef-dependent families such as Chaetodontidae, Labridae, and Acanthuridae are routinely absent from inshore collections (Leis and Miller 1976). McGowan (1985) found total larval abundance was highest at the eastern end of the Flower Garden Banks, in the downstream direction of the mean current flow. Reef-associated larval densities appear to follow this general pattern, with the eastern-most GC18 (most downstream platform, given the general west to east flow at the shelf-break as reported by McGrail et al. 1982) receiving greater amounts of supply than EB165. Increasing numbers of reef-associated larvae were also found offshore along

the cross-shelf transect. A similar pattern of reef-dependent supply is evident along the onshore-offshore transect, although no east-west differences between the shelf-break platforms were evident.

The low densities of reef-dependent larvae identified in this study are indicative of patchily distributed ichthyoplankton (Doherty et al. 1985). Richards (1984) noted that for many reef-dependent families from the Caribbean, their pelagic larvae were widely distributed, yet not very abundant. In an effort to better represent these spatially disjunct patches, Clarke (1991) suggested that very large volumes of water (on the order of 10^5 - 10^6 m^3) must be filtered in order to collect statistically adequate numbers of reef-fish larvae in open ocean systems. The passive-method surface nets used for this study filtered substantially less water (3.7×10^4 m^3).

Yet simply filtering vast quantities of water alone may still not completely reveal patterns of larval supply, because many larger-scale ichthyoplankton surveys have also reported reef-dependent densities at or near the range I found. Of the greater than 90,000 shorefish larvae taken during a seasonal survey around the Oahu, Hawaii, reef-dependent families (Acanthuridae, Chaetodontidae, Labridae, Pomacanthidae, Pomacentridae, and Scaridae) accounted for only 2.4% of the total (Leis 1991c, Table 3.1). Powles (1975) reported still lower percentages of reef-dependent families (1.9%) taken during a yearlong study of the ichthyoplankton around Barbados. These percentages were of the same magnitude as the percentage of reef-dependent larvae identified in this study (1.4%).

While light traps and plankton nets operate on very different principles (plankton nets actively strain larvae from the water while light traps rely on the physical/sensory capabilities of larvae to be drawn towards the trap), many studies have reported overall similarities in catch composition between the two gears (Doherty 1987b; Choat et al. 1993; Brogan 1994). Around platforms, I found little agreement in the kinds of larvae collected with these two gears. During 1994 and 1995, 43 different taxa were taken with the surface net, while only 3 taxa (clupeids, myctophids, and gobiids) were collected with the light traps. Only the most numerically abundant ichthyoplankton (clupeids) were collected from the surface trap. The low catch rates encountered by both the surface and deep light traps (0.1 - 0.6 individuals / hour) are quite different from other studies sampling with similar gear. In collections taken from Barbados, Cowen (1996) collected reef fish larvae in the range of 10 to 250 individuals / trap set, with mean species richness ranging from 6 to 24 species / set (see Sponaugle and Cowen 1996, Fig. 5). Doherty's (1987b) traps were highly effective in collecting settlement-stage pomacentrid larvae from the Great Barrier Reef, whereas Choat et al. (1993) collected numerous pomacentrid, gobiid, mullid, and labrid larvae and juveniles with a similar trap from Lizard Island.

Reef-dependent families were conspicuously absent from the shelf-break platform collections from either light trap (surface and deep trap), despite the juveniles and adults of these taxa being dominant members of the platform community (e.g., *Acanthurus coeruleus* - Acanthuridae; *Bodianus pulchellus* and *Thalassoma bifasciatum* - Labridae; *Abudefduf saxatilis*, *Chromis multilineata*, and *Pomacentrus*

partitus – Pomacentridae, see Gallaway and Lewbel 1982). The absence of these taxa from both the light trap and surface net collections may been due to a limited recruitment duration (e.g., all individuals recruit over a period of a few days; see Dennis et al. 1991), and if so, they may have not temporally overlapped with the quarterly sampling schedule utilized for this study.

One factor that may have led to such disparate results in light trap collections between this study and others sampling with similar gear is the speed of the surface current moving past the platform, carrying larvae past the illuminated trap before they had an opportunity to enter the trap chamber. During light trap sampling, surface currents at GC18 averaged 24.8 cm s^{-1} (SD = 14.8). Surface current velocities were typically lowest during the midnight period, with currents during the other diurnal sampling times ranging from 12.4 to 75.5 cm s^{-1}. Because the gap opening leading into the illumination chamber was on the order of 10 mm wide, larvae approaching the trap at speeds in excess of 20 cm s^{-1} had little chance of swimming back to the trap if it missed on the initial pass.

Another possible explanation for the low catch rates could have been the choice of the light source itself, a directional underwater dive light. Unlike many studies that have used outwardly radiating light sources (Doherty 1987; Choat et al. 1993; Brogan 1994; Thorrold and Williams 1996; Hernandez and Lindquist 1999), the halogen bulb dive light I used did not have a sphere of illumination capable of radiating a full 360°. This could help explain why the surface light trap collected only the most abundant family found in the plankton (Clupeidae).

In contrast, the high light trap catch rates reported by Doherty (1987b) were from free-floating traps, traveling at the same speed and direction as the surface currents. The deep trap, fished in the lower currents in the well bay, caught nearly twice as many larvae as the surface trap. Though lacking a record of depressed current speeds within the well bay, the greater number of larvae collected from the deep trap could be taken as evidence of increased trap efficiency. While the deep trap caught numerically more larvae, they too were families regularly encountered in the plankton (Myctophidae and Gobiidae).

An additional factor competing for the 'attention' of photopositive reef-fish larvae was the light traps themselves were fished within a much larger light trap (i.e., the platform itself). At night, numerous floodlights (in addition to the lights of the superstructure and the pressure relief gas flare) illuminate the lower decks as well as the surrounding surface waters. These light sources could be essentially acting as a larger light aggregation device. With the combination of strong surface currents and the competing platform floodlights (light intensity within the trap chamber was far lower than the platform floodlights), the surface trap proved to be ineffective. At -20 m depth, the intensity of the floodlights was substantially less and the deep-set light trap was relatively more effective.

The change in gear from light traps to lighted plankton nets merely reinforced both the spatial and temporal supply patterns identified for reef fishes around petroleum platforms: spring maximum seasonal supply (with a smaller, secondary peak in the fall for reef-dependent families), and summer maximum supply for reef-associated families.

Because the illumination source for the lighted plankton net was substantially brighter than the light trap (a three dive light array on the lighted plankton net vs. a single light for the light trap) and the surface net circumvented current velocity problems, behavioral responses to this light aggregating device could be seen for some families. Cynoglossids (10-13 mm SL) and synodontids (4-29 mm SL) were attracted to the lighted plankton net, whereas scombrids appeared to be able to actively avoid the lighted net despite their much smaller developmental size (3-7 mm SL). Reef fish species that showed a photonegative response included the serranids, opistognathids and blenniids. No reef families showed any strong photopositive response.

Very few larvae of the most conspicuous coral reef fishes were encountered in the plankton (Pomacanthidae, Chaetodontidae, Labridae, and Scaridae), despite each of these families being well represented as adults on the platform habitats. The small size of individuals that were collected from the surface waters is indicative of local spawning. Whether the supply of these individuals to the platforms is infrequent and dictated by unusual oceanographic events, or is regular and reliable but at a frequency that did not coincide with the quarterly sampling schedule of this study, could not be determined.

CHAPTER 2: REMOTE SENSING INVESTIGATIONS OF REEF FISH ICHTHYOPLANKTON SUPPLY ON THE CONTINENTAL SHELF: OBSERVATIONS ON POSSIBLE SOURCE LOCATIONS

Introduction

Dispersal and recruitment play a pivotal role in the population dynamics of many reef fishes, because these organisms often live in disjunct, patchy environments and produce pelagic offspring that disperse among patches (Sale 1980). The survival of the early life history stages of reef fishes is greatly influenced by processes acting upon them during their planktonic transport (Kingsford 1993), and recruitment success often plays a pivotal role in the dynamics and abundance of local populations (Victor 1983, 1986b; Rosenblatt and Waples 1986; Lewin 1987; Mapstone and Fowler 1989; Jones 1990; Doherty and Fowler 1994a, b; Sponaugle and Cowen 1997; Tolimieri et al. 1998). One prevailing hypothesis of reef fish recruitment argues that major settlement events occur when occasional dense patches of planktonic larvae encounter appropriate habitats (Thorrold and Williams 1996).

The length of the pelagic life-phase in reef fishes varies from several days to several months and it is thought that early-life history attributes play an important role in their effective dispersal distance (Brothers and Thresher 1985; Thresher et al.1989; Underwood and Fairweather 1989; Wellington and Victor 1989; Victor 1991a). The distance an organism can travel during dispersal also has important effects on gene flow and genetic differentiation, as well as the geographical extent and numerical size of an interbreeding population (Lascon 1992; Shulman and Bermingham 1995; Roberts

1997). The spatial area of enhanced settlement and the frequency of settlement events relative to the life cycle of reef-dependent fishes will determine not only local population structure, but also that of the larger metapopulation (defined as a collection of smaller, relatively independent subpopulations occurring within a system of interconnected patches; see Hanski 1991, Man et al. 1995).

The tropical ichthyofaunas found on natural reef sites in the Gulf of Mexico (Gulf) are thought to have originated from inflows of Caribbean water carrying eggs and larvae (Bright and Cashman 1974, Rezak et al. 1990; see Fig. 28). The emergent and submergent hermatypic reefs found on the west Florida Shelf (including the Florida Middle Grounds, Dry Tortugas, and the Florida Keys) and the Yucatan Shelf (including Alacran, Cayo Arenas, and Triangulos reefs) all share the characteristic of being floored by carbonate sediments (Rezak et al. 1985). Throughout the remainder of the Gulf, terrigenous sediments with varying amounts of silt and clay characterize reef sites.

The numerous submarine banks (drowned coral/algal reefs built on relict carbonate shelf banks south of Matagorda Bay, Texas, as well as salt diapir expressions east of Matagorda Bay on the Texas-Louisiana outer continental shelf, Fig. 29) found in the northern Gulf have communities dominated by coralline algae, ahermatypic corals, antipatharians, and deep-water alcynarians. Although long-range transport mechanisms were once thought to maintain these reef fish populations, recent studies have shown that the ichthyofaunas associated with these habitats are resident populations (Parker and Curray 1959; Cashman 1973; G.B. Smith 1976; McGowan

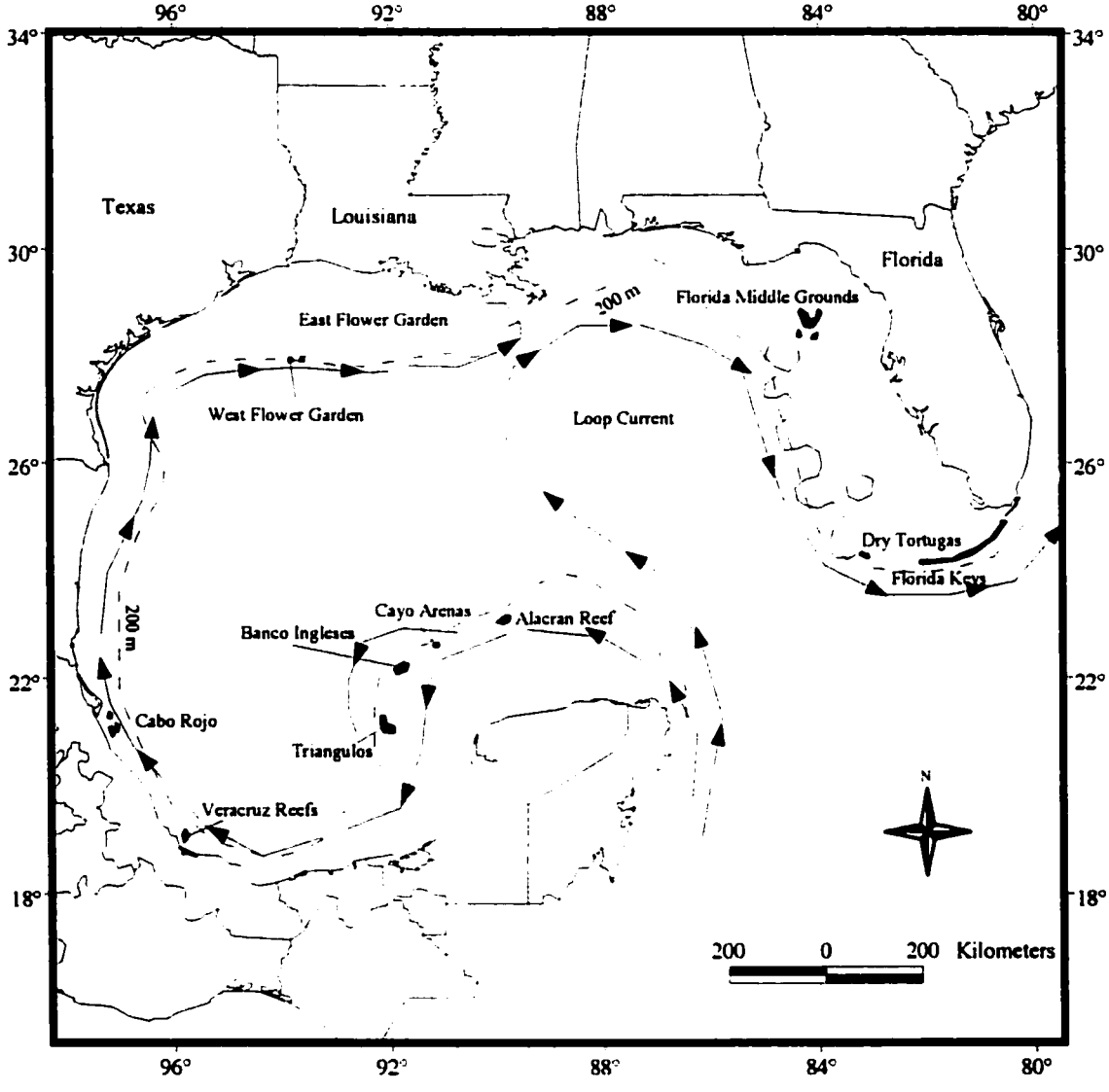


Figure 28. Near-surface circulation patterns that may be responsible for carrying biotic communities into the Gulf either anti-cyclonically around the western Gulf or via the Loop Current and spin-off eddies, to the Florida Shelf. Coral reefs of major biogeographical significance are identified. (Modified from Rezak et. al. 1985).

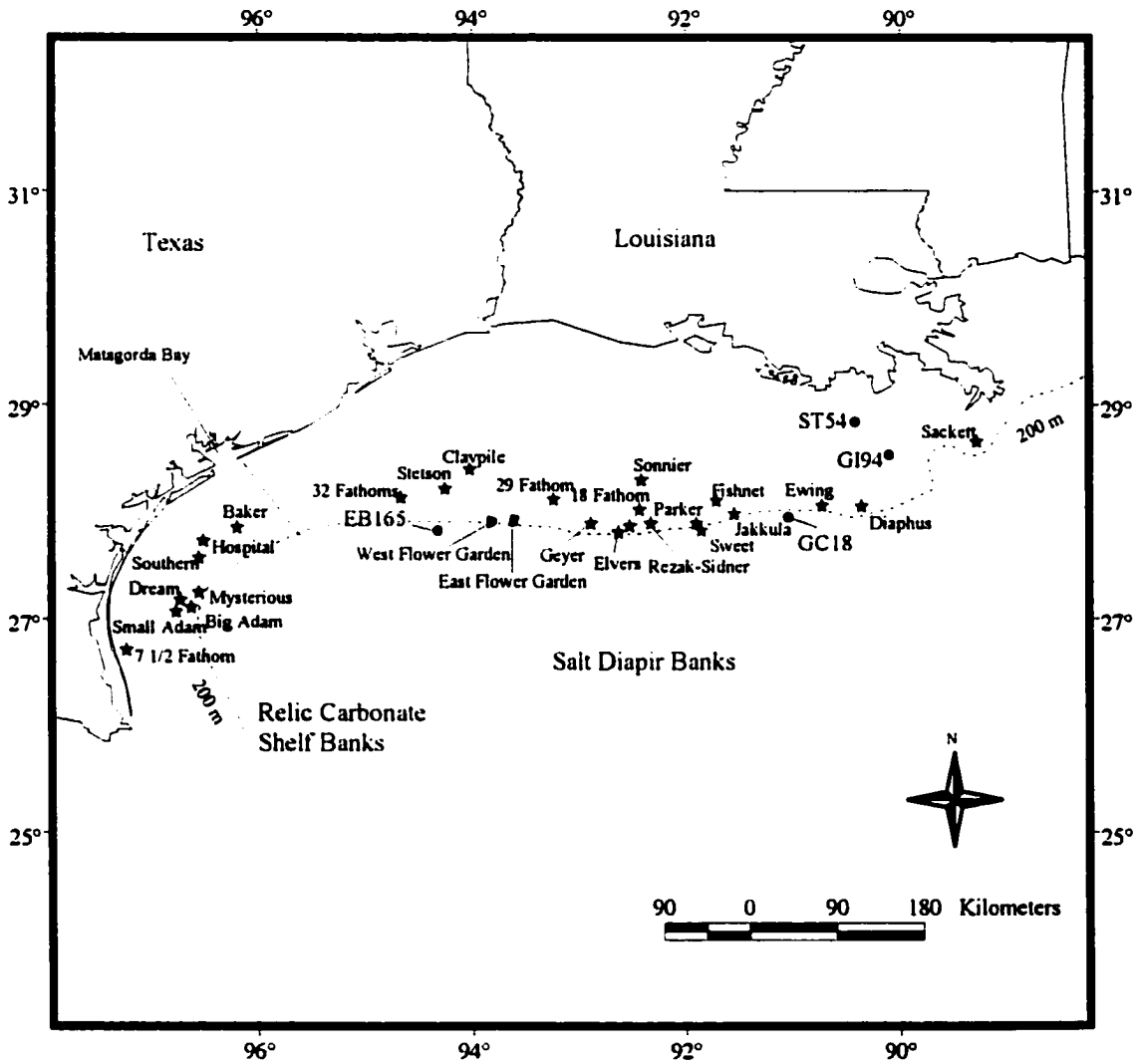


Figure 29. Locations of salt diapir and relic carbonate shelf banks in the northern Gulf of Mexico in relation to the four sampling platforms. Physical characteristics of selected banks and reefs are presented in Appendix C. Solid line denotes dividing line between relic carbonate and salt diapir submerged bank habitats.

1985; Dennis and Bright 1988). Attributes of local current patterns may act to retain eggs and larvae, or to transport them to other nearby sites of suitable adult habitat (e.g., along a coast or moving in a stepping-stone fashion along a series of submerged banks).

Within the Gulf, the dominant circulation feature is the Loop Current, the portion of the Gulf Stream System that enters the Gulf from the Caribbean through the Yucatan Channel and exits through the Straight of Florida (Maul et al. 1978). Large-scale circulation features associated with the Loop Current that have the potential to modify reef-fish larval transport are the numerous eddies generated when the northward intrusion separates from the rest of the Loop Current (Lamkin 1997). These large (200-300 km at formation) anticyclonic, warm-core rings are pinched off from the Loop Current and move into the western Gulf where they eventually spin down and break up (Merrell and Vazquez 1983; Lewis 1992). As the warm-core eddies move westward, adjacent mesoscale (20-80 km) cyclonic cold core rings (CCR) may develop (Merrell and Vazquez 1983; Lewis and Kirwan 1985; Hamilton 1992). In the eastern Gulf of Mexico, these cyclonic rings occur in close association with the Loop Current (Lee et al. 1994), and in the central and western Gulf, they are companions of the westward moving anticyclonic formations (Rouse et al. 1994). Anticyclonic ring separation occurs every 6-17 months, averaging one new eddy every 11 months (Elliot 1982). Multiple anticyclonic eddies may exist simultaneously within the central and western part of the Gulf, each in various stages of decomposition as they spin down. The interactions between anticyclone-cyclone systems moving within the Gulf have

been recognized for their biological importance in terms of increased primary production (Hamilton 1992; Biggs and Muller-Karger 1994; Biggs et al. 1997), higher abundance of larval fishes (Lamkin 1997; Limouzy-Paris et al. 1997), and increased catch per unit effort of large pelagic predators (Maul et al. 1984).

The Loop Current, however, is not the primary factor influencing larval fish transport over the continental shelves (Fig. 30). For example, the Texas-Louisiana shelf is dominated by a large cyclonic gyre driven by nearshore westward currents associated with local wind stress (N.P. Smith 1980; Crout et al. 1984). Near the shelf break, an eastward flowing countercurrent is present during most of the year (Cochran and Kelly 1986), although during summer (July and August) wind shifts cause reversals of flow and the gyre system breaks down. The Mississippi-Alabama Shelf is dominated by local wind forcing from the south and southeast during summer resulting in a westward flow, however, flow reversals from wind shifts are also noted (Chaung et al. 1982). Outer shelf water is frictionally driven eastward by Loop Current intrusions. These nearshore and offshore transport mechanisms form a semi-permanent cyclonic gyre over the Mississippi-Alabama Shelf (Schroeder et al. 1987). Longshore currents primarily dominated by local wind stress (Marmorino 1983) characterize the inner West Florida shelf, whereas the mid- and outer-shelf areas are dominated by geostrophic flows extending out to the shelf break (Mitchum and Sturges 1982). Mean flow along the outer West Florida shelf is to the south during the summer.

The objective of this study was to investigate which macro- or meso-scale larval transport mechanisms potentially control the distribution and abundance of reef-fish

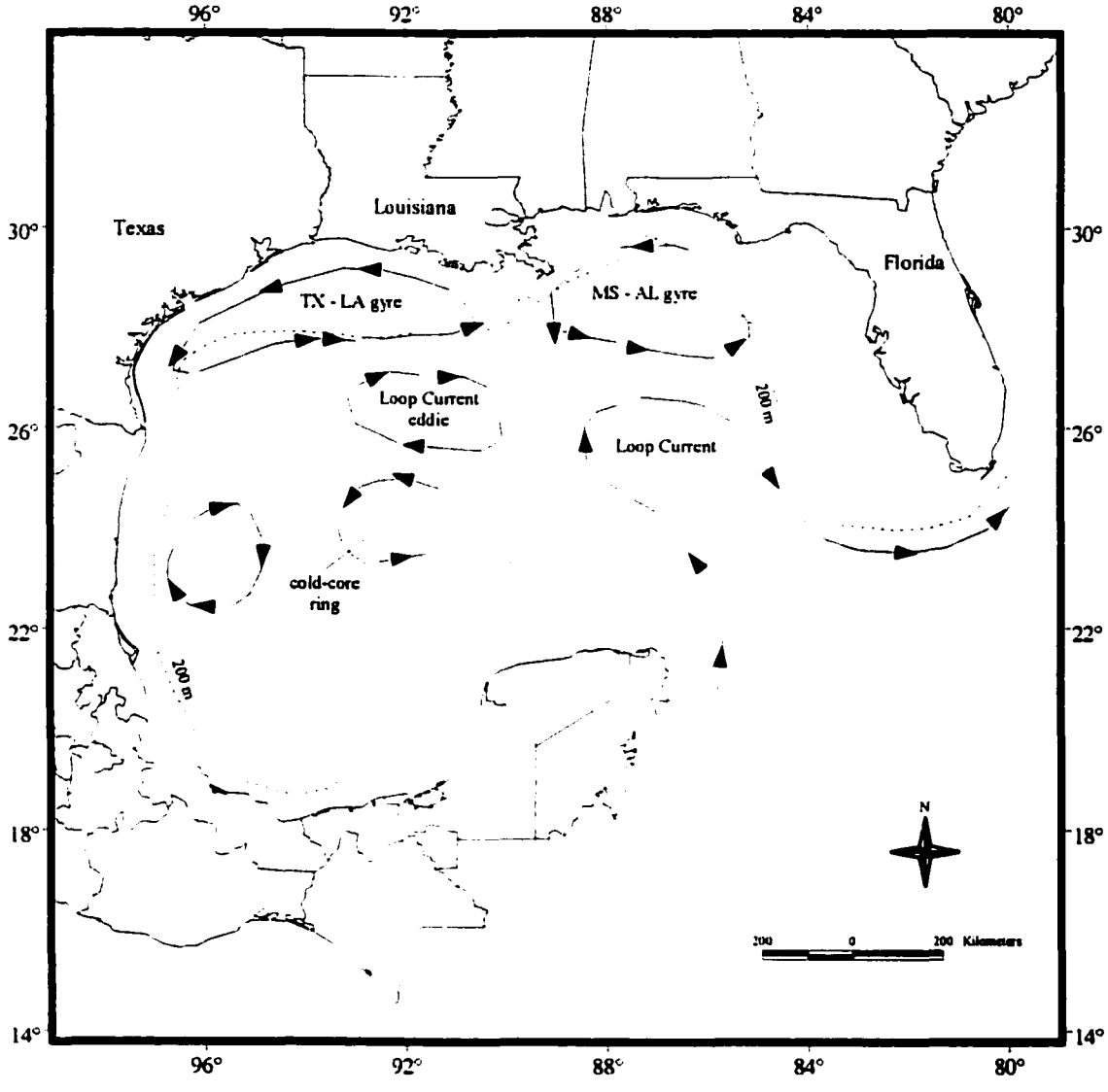


Figure 30. Idealized representations of the major water mass circulation components that could influence larval transport and reef-fish distributions within the Gulf.

species supplied to artificial reef sites in the north-central Gulf. Specific questions asked to achieve this objective included (1) which major circulation features in the northern Gulf could have determined seasonal supply of reef-dependent larvae to platform habitats during 1996 and 1997; (2) how old are larvae from a representative reef-dependent family when they arrive at a platform; and (3) what locations are potentially serving as recruitment sources for reef-dependent fish taxa?

Methods and Materials

Planktonic transit-time calculations were performed on the most abundant reef-dependent family collected from the ichthyoplankton (Serranidae; see Chapter 1, Results). Larvae preserved in 95% ethanol were identified to the lowest possible taxon and then measured to the nearest 0.1 mm with an ocular micrometer on a dissecting microscope. Lengths are notochord length for pre-flexion larvae and standard length for flexion and post-flexion larvae. No correction to account for shrinkage was applied. If an individual species dominated the catch from a particular trip, representative individuals were randomly selected from the total collection, and those were then used for age determination and transit-time calculations.

Both left and right sagittal otoliths were excised under a dissecting microscope with transmitted cross-polarized light, rinsed in water, air-dried and mounted whole (concave side down, unpolished) in Permount on a glass microscope slide. Unless damaged during processing, or determined unreadable (see below), only the left sagittal otoliths were read. Otoliths were sufficiently thin to allow for optical sectioning (focusing to the plane of maximum clarity to make total increment counts) at 400× to

1000× magnification under cross-polarized light through a compound microscope. Presumed daily increments were counted from the initial ring surrounding the primordium to the margin of the otolith along a consistent axis. Two independent counts were made; each without prior knowledge of fish length or any prior age determination. Incomplete marginal increments were not counted. In cases where the first two counts differed, a third independent count was performed, and the consensus age corresponded to the two counts that agreed. If no agreement could be reached, the otolith was considered unreadable and the right otolith was processed. If no agreement could be reached on the right otolith, the fish was excluded from the analysis.

Large-scale circulation features impacting the mid-shelf and shelf-break study platforms (GI94, GC18, and EB165) were investigated with radar altimeter data provided by the University of Colorado, Colorado Center for Astrodynamics Research (CCAR). Several authors have found good agreement between currents estimated with altimeter data and ground-truthing (Ma et al. 1994; Yu et al. 1995; Mitchum 1996). Maps of the sea surface height anomaly with superimposed geostrophic flow velocity vectors produced from blended TOPEX/POSEIDON (hereafter T/P) and ERS-2 altimeter satellite passes were obtained from CCAR (Fig. 31). The processing is designed to retain the mesoscale sea surface height anomalies associated with fronts and eddies (Fu et al. 1994). An analysis image is produced daily, based on the previous 10 days of T/P and 17 days of ERS-2 sampling. Because the geoid is not known, a model estimate of the mean dynamic topography was added to the sea surface height

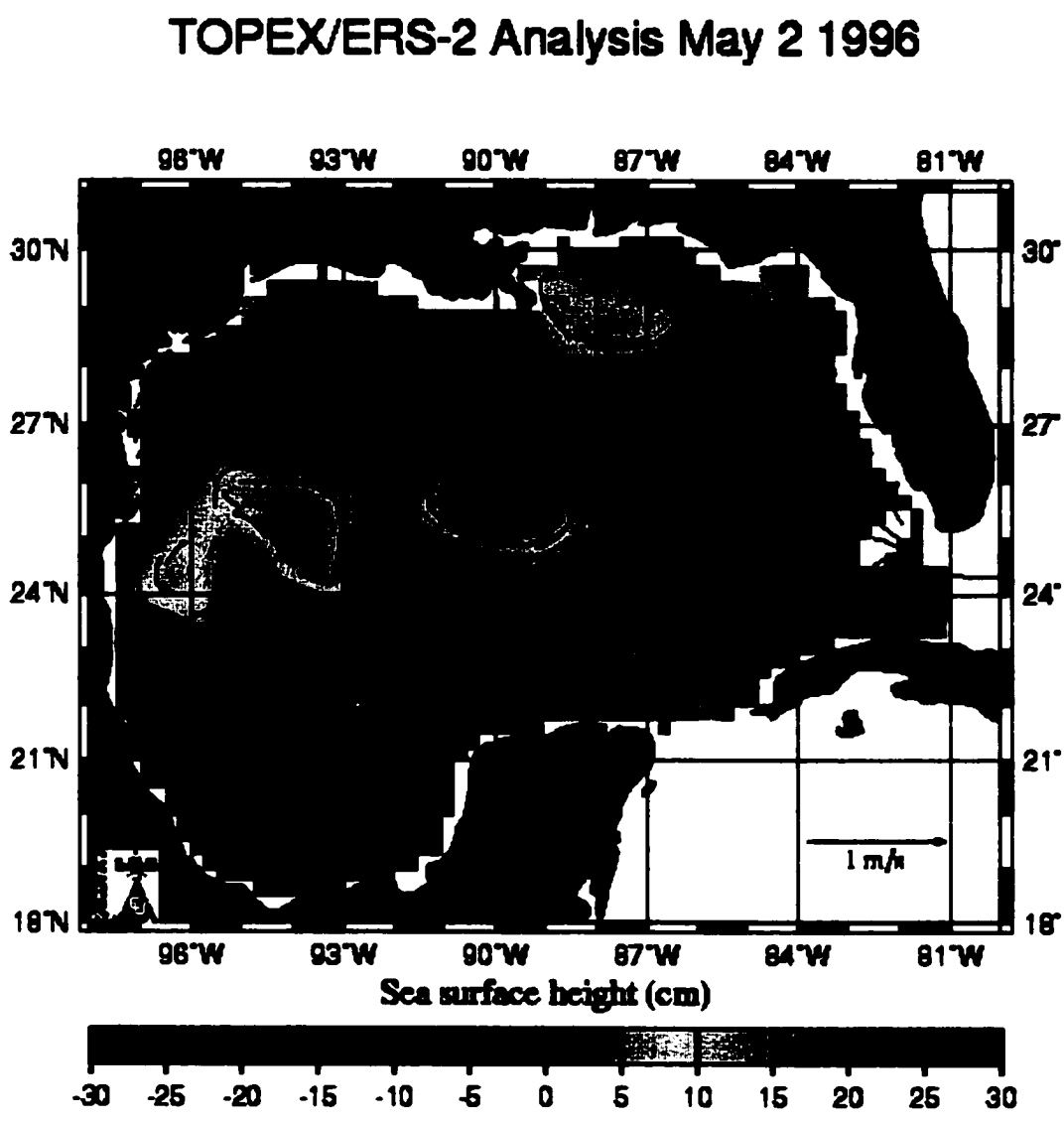


Figure 31. Sea surface height and geostrophic current estimated from the blended TOPEX/POSEIDON and ERS-2 altimeter observations. Data provided by CCAR.

anomalies. The long-term mean dynamic height at 1000 m depth, which was assumed to be representative of the mean dynamic topography, originated from the 1995 Ohio State University Mean Sea Surface data (Yi 1995). A smoothing radius of 50 km was applied to interpolate the irregularly spaced satellite tracks onto a uniformly spaced latitude-longitude matrix.

Satellite altimeter remote sensing is a useful tool in studying oceanographic conditions relevant to larval transport (Stegmann and Yoder 1996; Polovina et al. 1999). Estimating lateral movement of larvae in the surface waters from blended T/P and ERS-2 altimeter data circumvented image availability problems due to cloud cover (e.g., sea surface temperature, see Lillibridge et al. 1997), and helped to resolved the internal motions associated with eddy propagation. Still, this approach does have limitations. As pointed out by Polovina et al. (1999), the spacing between the satellite tracks, especially in the mid- and low-latitude regions, may be too broad to completely resolve many finescale and mesoscale physical features relevant to larval transport. Additionally, the mean topographical dynamic height added to the model varies depending on the spatial and temporal distribution of the data, thus it is likely that these biases may have had an impact on the estimates of geostrophic currents. Finally, an altimeter-derived approach in determining the spatial extent of larval movement is most appropriate in situations where geostrophic transport is the most significant source of larval transport, that is, in situations where larvae are below the shallow Ekman layer (Polovina et al. 1999).

Daily contour maps of the dynamic sea surface height with superimposed geostrophic current velocity vectors were compiled for the period of April 1996 to May 1997 (time period of concurrent surface ichthyoplankton samples and altimeter image availability from CCAR). From these maps, the daily current speed (in cm/s) and direction (mean angle) at each study platform was calculated. In situations where the current vector was curved, I applied a linear interpolation of the curve to determine both the velocity and direction. Daily direction and velocity values were then aggregated into 14-day running-average resultant vectors at each platform (14-day cycles represented the mean age at capture of the serranids arriving in the plankton; see Results, Fig. 33). Based on these resultant vectors, I then determined the probable supply area as the lateral distance (in km) of how far the larvae could have traveled. This was done for each 14-day series within each season (winter, spring summer, and fall), and all seasonal supply points were then connected to form a seasonal transport polygon. Because estimated surface currents derived from altimeter images are appropriate only in situations where geostrophic flow is a significant component of larval transport (Polovina et al. 1999), only the shelf-break platforms (EB165 and GC18) and the mid-shelf platform (GI94) were used for this analysis.

A map of the 4,359 platform structures in the northern Gulf was constructed with data provided by the Minerals Management Service, Gulf of Mexico OCS Region (Fig 32). This primary map was used as a Geographic Information System (GIS) foundation in order to build subsequent spatial layer maps to compare the seasonal

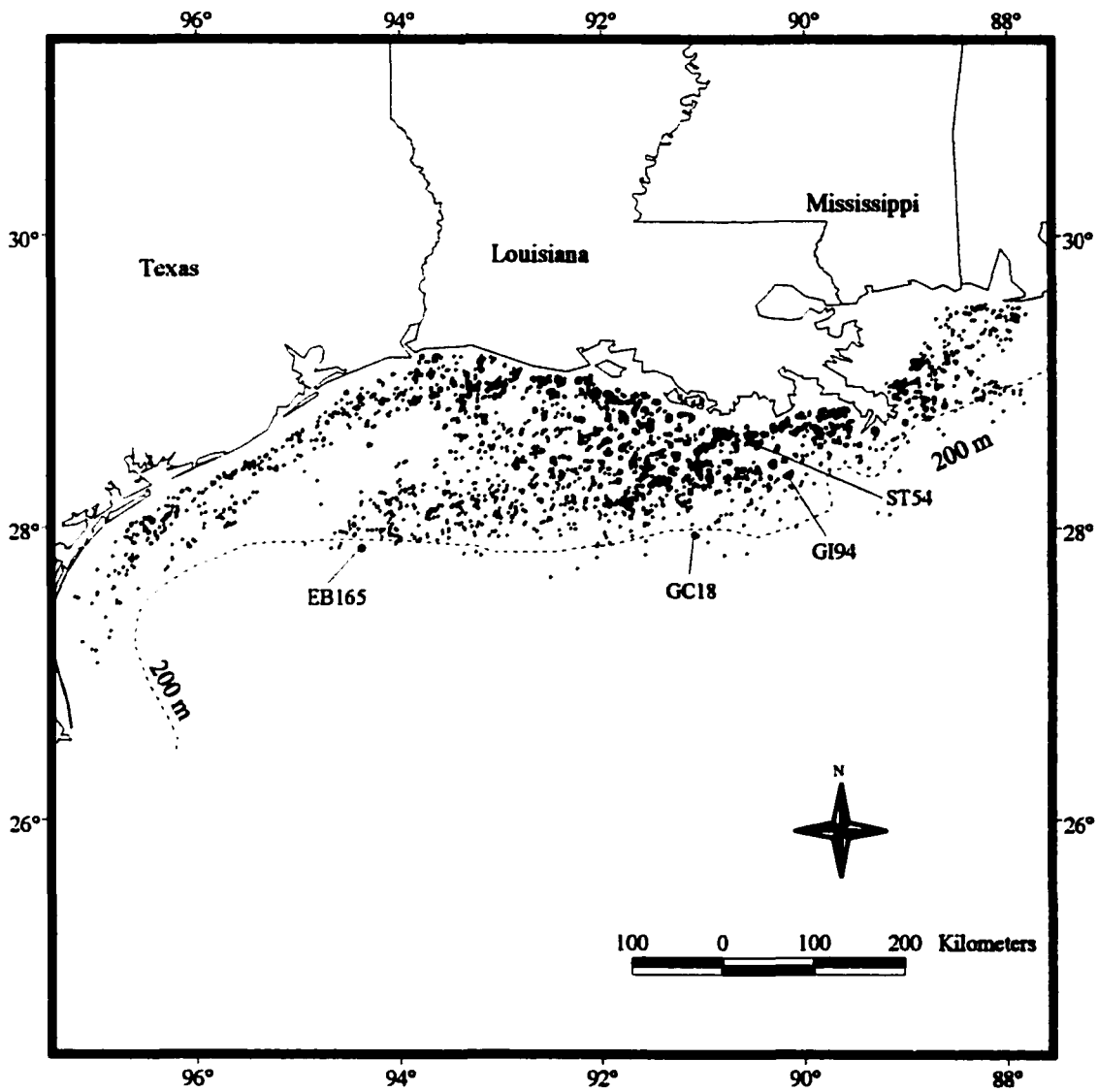


Figure 32. Map of all oil and gas platform structures (number of offshore platforms during the period of this study, N = 4,359) located on the continental shelf and shelf break area of the northern Gulf.

transport polygons defined T/P – ERS-2 derived surface current fields. Additional GIS layers of the large, natural reef sites, (as well as other hard-bottom reef sites) within the northern Gulf were complied.

Statistical Analysis

If a common source were supplying reef fish larvae to artificial reef platform habitats, recruiting fishes would be in transit for varying amounts of time in order to reach each platform. Platforms nearer the common source should have smaller sized individuals being supplied to them, because these larvae would conceivably spend a shorter amount of time in transit. Therefore, the mean size at capture of reef fish larvae (Serranidae) were compared among platforms with a one-way ANOVA.

Because the family-level grouping consisted of a mixture of taxa recruiting over different seasons, sub-family differences in estimated age at capture were further assessed with an analysis of covariance (ANCOVA). Family-level designations were separated into sub-family groupings and tested for differences in mean age at capture. Additionally, seasonal differences in mean age at capture were assessed. Probable source areas were then identified based on the average time in the plankton (mean age) necessary to reach the mid-shelf and shelf-break platforms.

Statistical methods for describing the seasonal current direction (mean angle) and dispersion (mean angular deviation) follow those found in Zar (1984). The quantity *s*, or mean angular deviation, ranges from a minimum of 0° (no dispersion in the mean angle) to a maximum of 81.03° (the mean angle is undefined and there is no mean direction). This measure is analogous to the standard deviation on a linear scale.

Because angular deviation is measured on a fixed circular scale, it is bounded by a finite upper limit (Zar 1984).

Results

Transit Time Calculations

The complete serranid collection was composed of 13 identifiable species/species complexes, shown in Table 12. The Anthiinae (primarily *Anthias nicholsi*) were numerically dominant from both shelf break platforms, and these were encountered primarily during the spring season. The two other abundant subfamilies (Serraninae and Epinephelinae) were found in greater numbers in the eastern portion of the study area (i.e., GC18 and GI94), with fewer numbers of both taxa and individuals found at the mid-shelf platform. Soapfish larvae (Grammistinae: *Rypticus* spp.) were encountered only from the western shelf-break platform at EB165.

Mean size of serranids collected from the surface waters did not differ significantly among the three platforms (mean = 3.82 mm TL, SD = 1.09; $F_{(2, 314)} = 1.95$; $p = 0.14$). The residuals were not normally distributed (W:Normal = 0.93; $p < 0.001$), with the distribution positively skewed due to six large *Diplectrum* spp. and two *Paranthias furcifer* individuals collected from GI94 and GC18, respectively. Because the number of individuals collected from GI94 was an order of magnitude less than either shelf-break platform, I excluded all serranids from the mid-shelf platform and again tested for mean size differences between EB165 and GC18 alone. Based on an unequal variance t test, no significant differences were found ($t = 1.96$; df = 255.2; $p = 0.051$).

Table 12. Total number of each serranid species or species complex, collected by platform and season, used in the back-calculation otolith aging method. Seasons not sampled during 1996 - 1997 denoted with n/a. Subfamily designations follow Eschmeyer (1990).

		EB 165			GC 18			GI 94		
Subfamily	N	Summer	Fall	Spring	Summer	Fall	Spring	Summer	Fall	Spring
Anthiinae										
Anthias nicholsi	59	0	n/a	19	n/a	0	40	0	0	0
Anthias woodsi	4	0	n/a	1	n/a	0	3	0	0	0
Hemanthias vivanus	8	0	n/a	2	n/a	0	6	0	0	0
Hemanthias leptus	3	0	n/a	2	n/a	0	1	0	0	0
Pronotogrammus martinicensis	11	0	n/a	7	n/a	0	4	0	0	0
Epinephilinae										
Epinephalus spp.	1	0	n/a	0	n/a	0	1	0	0	0
Mycteroperca spp.	3	0	n/a	1	n/a	0	1	0	0	1
Paranthias furcifer	5	0	n/a	1	n/a	0	4	0	0	0

Table 12. (cont.)

Subfamily	N	EB165			GC18			GI94		
		Summer	Fall	Spring	Summer	Fall	Spring	Summer	Fall	Spring
. Grammistinae										
Rypticus spp.	3	0	n/a	3	0	0	0	0	0	0
Serraninae										
Centropristis spp.	7	0	n/a	1	n/a	0	4	0	2	0
Diplectrum spp.	8	0	n/a	0	n/a	1	0	0	0	7
Serranus spp.	11	0	n/a	0	n/a	2	7	0	2	0
Hypoplectrus unicolor	1	0	n/a	0	n/a	0	0	0	0	1

The 13 species/species complexes averaged transit times of 14.5 days (mean = 10.5 rings, SD = 3.13, plus 4 days for initial ring formation; see Colin et al. 1997), and ranged from an estimated 7 to 27 days in the plankton (Fig. 33). Aggregated into their four respective subfamilies, covariance analysis revealed that no subfamily group showed any seasonal difference in average age at capture (although the numbers of larvae collected during the fall were an order of magnitude less than those collected during spring; see Fig. 33). No differences in intercepts (subfamily group adjustments; $F_{(1, 104)} = 1.33$; $p = 0.27$), nor slope × intercept interactions ($F_{(1, 104)} = 0.80$; $p = 0.495$) were detected for the four subfamily groups. Therefore, I used 14.5 days as the average transit time for serranid larvae arriving at each artificial reef platform to determine spatial resolution of probable supply areas.

Spatial Resolution of Possible Supply Areas

Surface current direction and magnitude at each study platform from summer 1996 to spring 1997 is presented in Fig. 34. The T/P and ERS-2 derived surface current fields at the study platforms were characterized by velocities ranging from 1.8 cm s^{-1} to 67.8 cm s^{-1}. Numerous reversals in the direction of flow are a prominent feature of the overall circulation, underscoring the complicated and often variable nature of circulation in this region of the Gulf of Mexico. Mean current flow (in terms of direction and magnitude) and measures of variation by season are presented in Table 13.

Prominent features potentially impacting larval fish transport to the study platforms that could be identified in each season were large, warm-core eddy

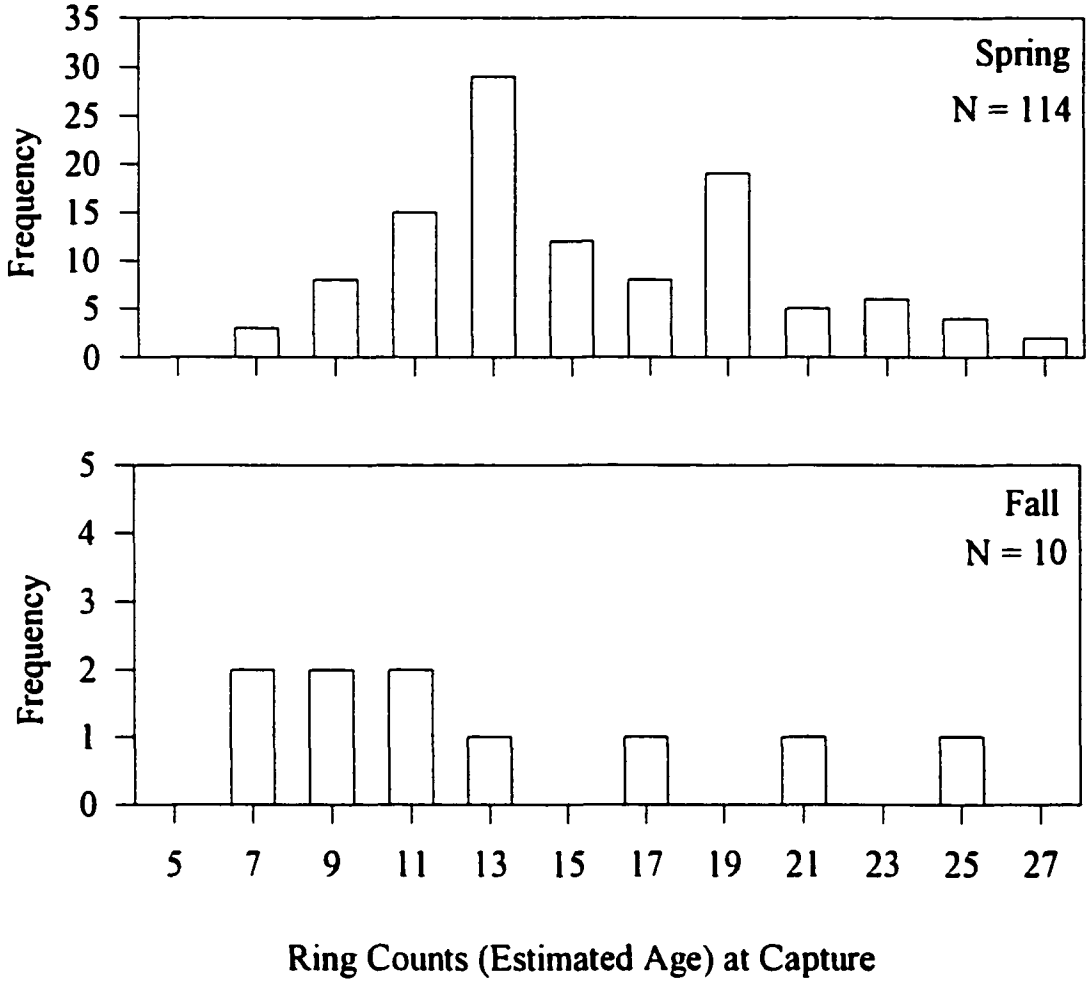


Figure 33. Seasonal comparisons of the ring counts at capture of Serranidae larvae (four subfamilies combined) from the mid-shelf and offshore platforms. Estimated age equals ring counts plus four. Note scale change of y-axis between spring and fall seasons. No larvae were collected during the summer season.

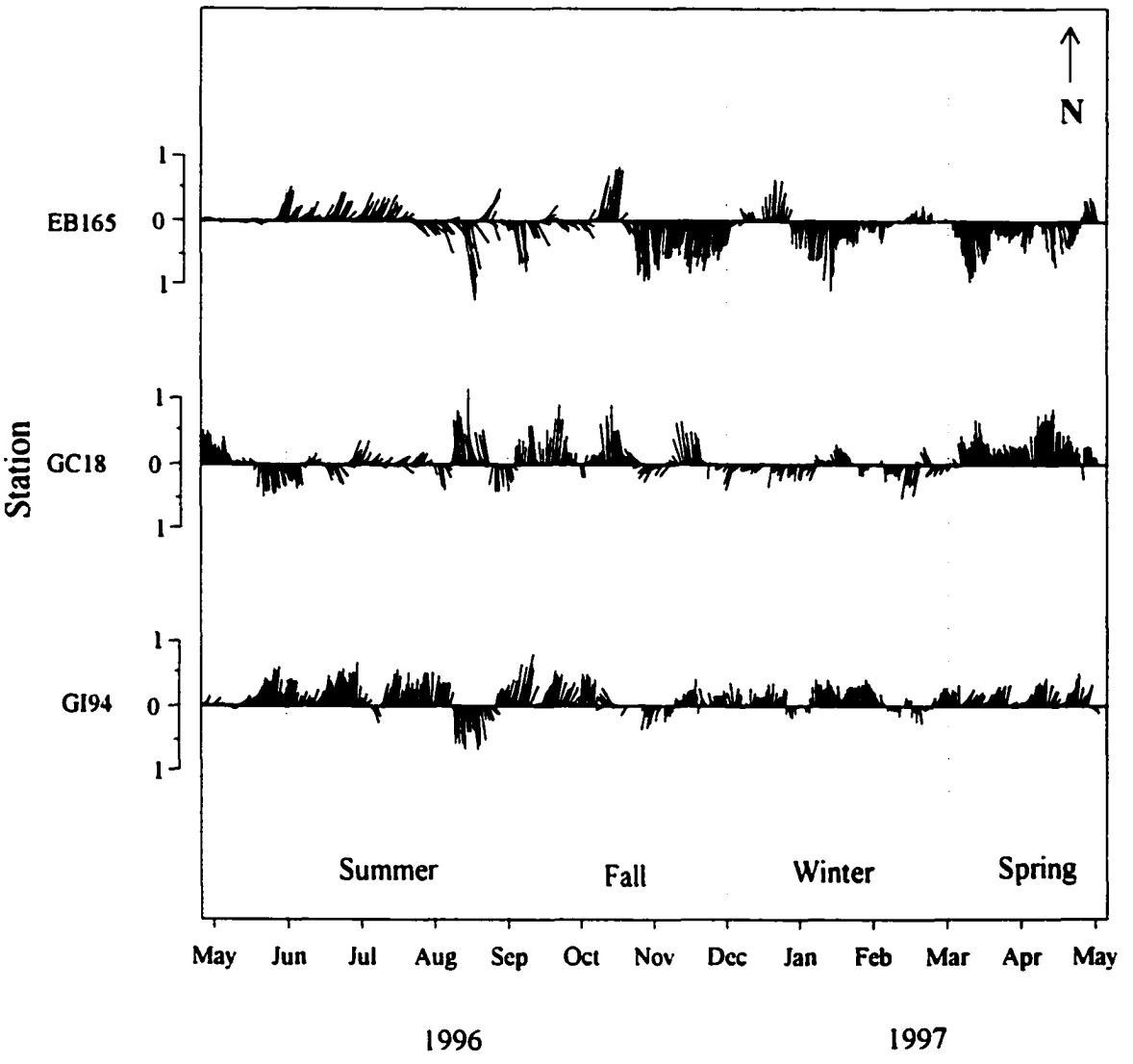


Figure 34. Vector time series (daily direction and magnitude) of surface current flow as derived from blended TOPEX/POSEIDON and ERS-2 altimeter data from 1996 and 1997. Vector length equals current magnitude (in m/s) and orientation equals current direction away from the x-axis.

Table 13. Blended T/P and ERS-2 derived seasonal mean surface current direction and flow at each study platform during summer 1996 to spring 1997.

Station	Season	Current Direction		Current Speed (cm / sec)	
		Mean Angle	Angular Dispersion	Mean	SD
EB 165	Summer	87.8°	16.9°	39.3	12.2
	Fall	120.2°	57.9°	34.0	7.4
	Winter	323.4°	63.9°	14.7	9.8
	Spring	130.4°	58.3°	18.8	9.5
GC 18	Summer	87.9°	50.6°	26.2	10.7
	Fall	333.3°	51.3°	25.6	12.8
	Winter	252.9°	42.2°	16.8	7.9
	Spring	307.2°	50.9°	18.3	5.8
GI 94	Summer	55.5°	45.3°	19.7	4.9
	Fall	350.6°	68.8°	20.6	12.4
	Winter	7.0°	65.5°	11.3	5.1
	Spring	65.1°	24.0°	19.4	5.2

formations migrating west beyond the outer margin of the continental shelf (generally centered below 26° N latitude; Fig. 35). Another feature easily identified in every season was a prominent cold-core ring that maintained its position north and west of the leading edge of the Loop Current, generally centered around 27° N latitude and 87° W longitude (see Fig. 35). Potential natal reef sites (natural reefs/ banks as well as other artificial reef platforms) for the 14.5-day moving average seasonal transport polygons are presented in Figures 36-39. Included with each seasonal polygon is an estimate of sea surface area (in square kilometers) defined by each polygon. Total numbers of potential supply areas by season, as defined by the T/P and ERS-2 derived polygons, are presented in Table 14.

During the summer period of 1996 the leading edge of the Loop Current was situated above 27° N, although it was confined to the eastern section of the Gulf, east of 87° W (see Fig. 35). By mid- to late summer, the western extent of this leading edge reached westward of 89° W, although it was never identified by the altimeter image series as migrating above 27° N latitude. Two prominent warm core eddies were identified in the beginning of the summer season, and they continued a westward migration along the outer continental shelf. Summertime eastward flow at GC18 was maintained in part due to the northern extend of these anti-cyclone features. While the transport polygon around GC18 was seasonally largest among the three platforms (see Fig. 36), and included the greatest number of natural reefs/banks, no surface net samples were collected from GC18 during summer. Mean flow at the mid-shelf

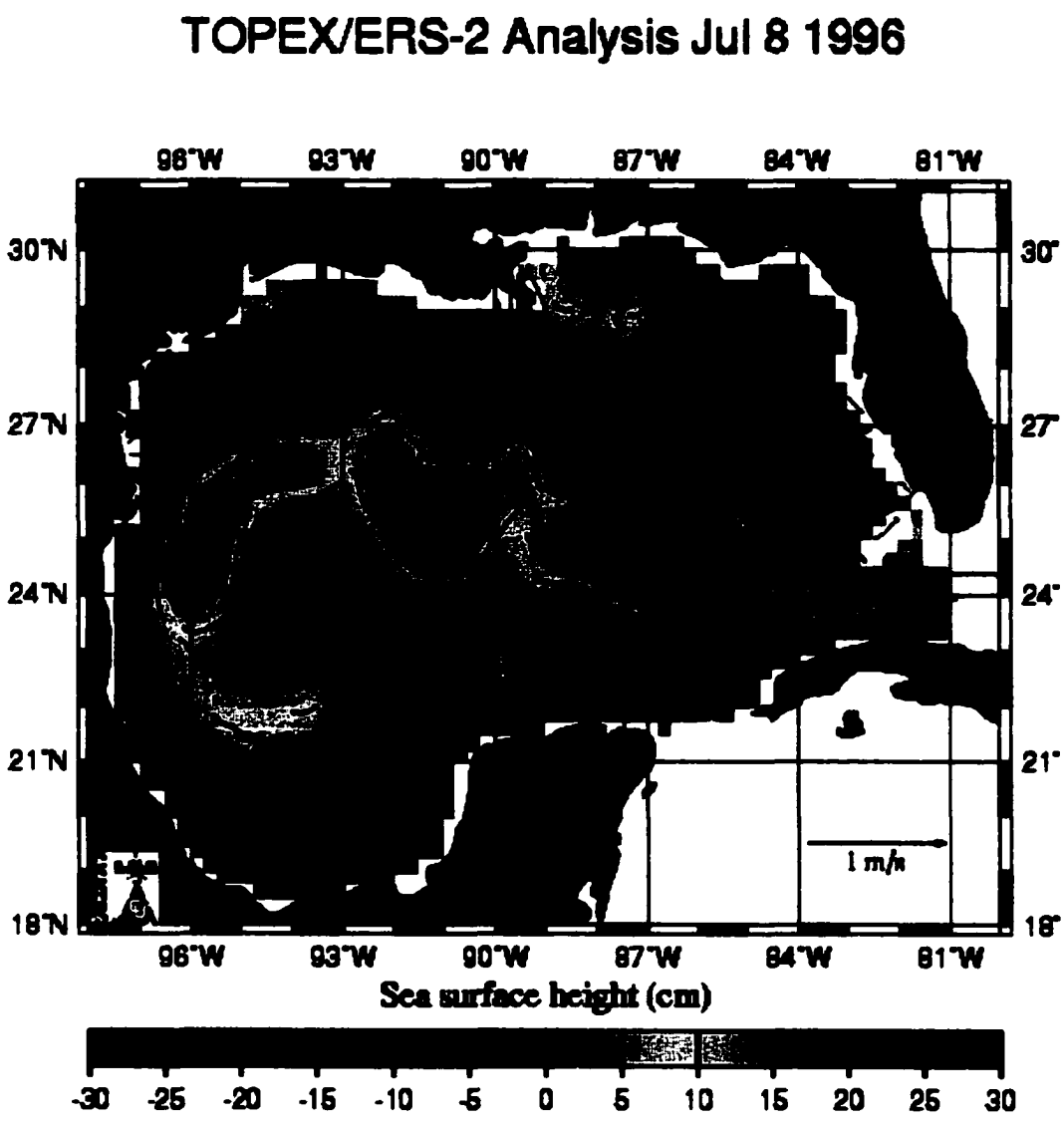


Figure 35. TOPEX/POSEIDON – ERS-2 image of the Gulf featuring prominent features potentially modifying reef fish transport to platform habitats, including the two warm-core eddies that were identified for the 1996-1997 period; the leading edge of the Loop Current, and the primary cold-core ring.

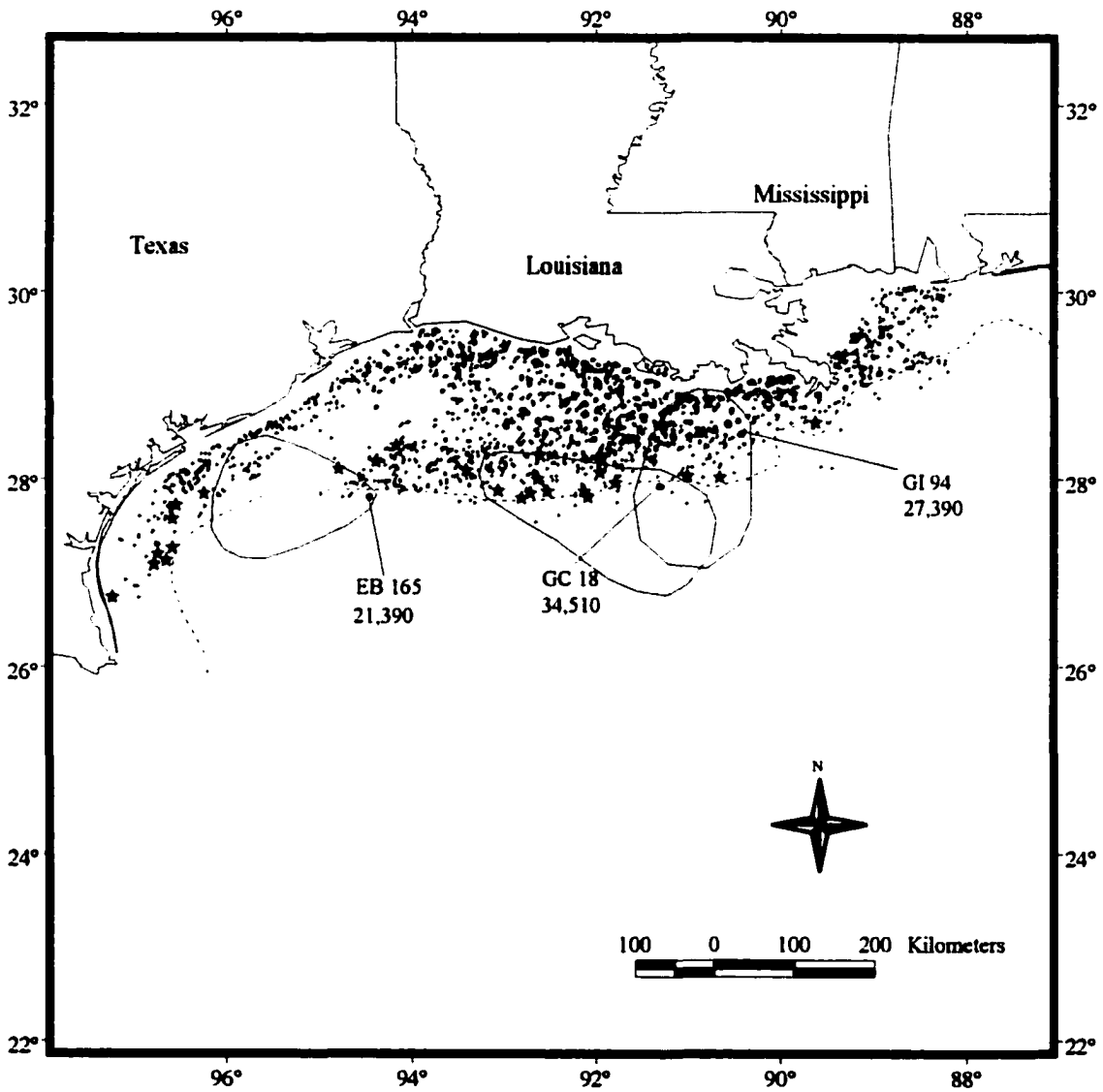


Figure 36. Seasonal transport polygons (including estimated spatial area in square km) for larvae arriving at the mid-shelf and shelf-break platforms, overlaid onto potential habitat sources (• = platform structures; ★ = natural reef sites) during the summer sampling period in 1996.

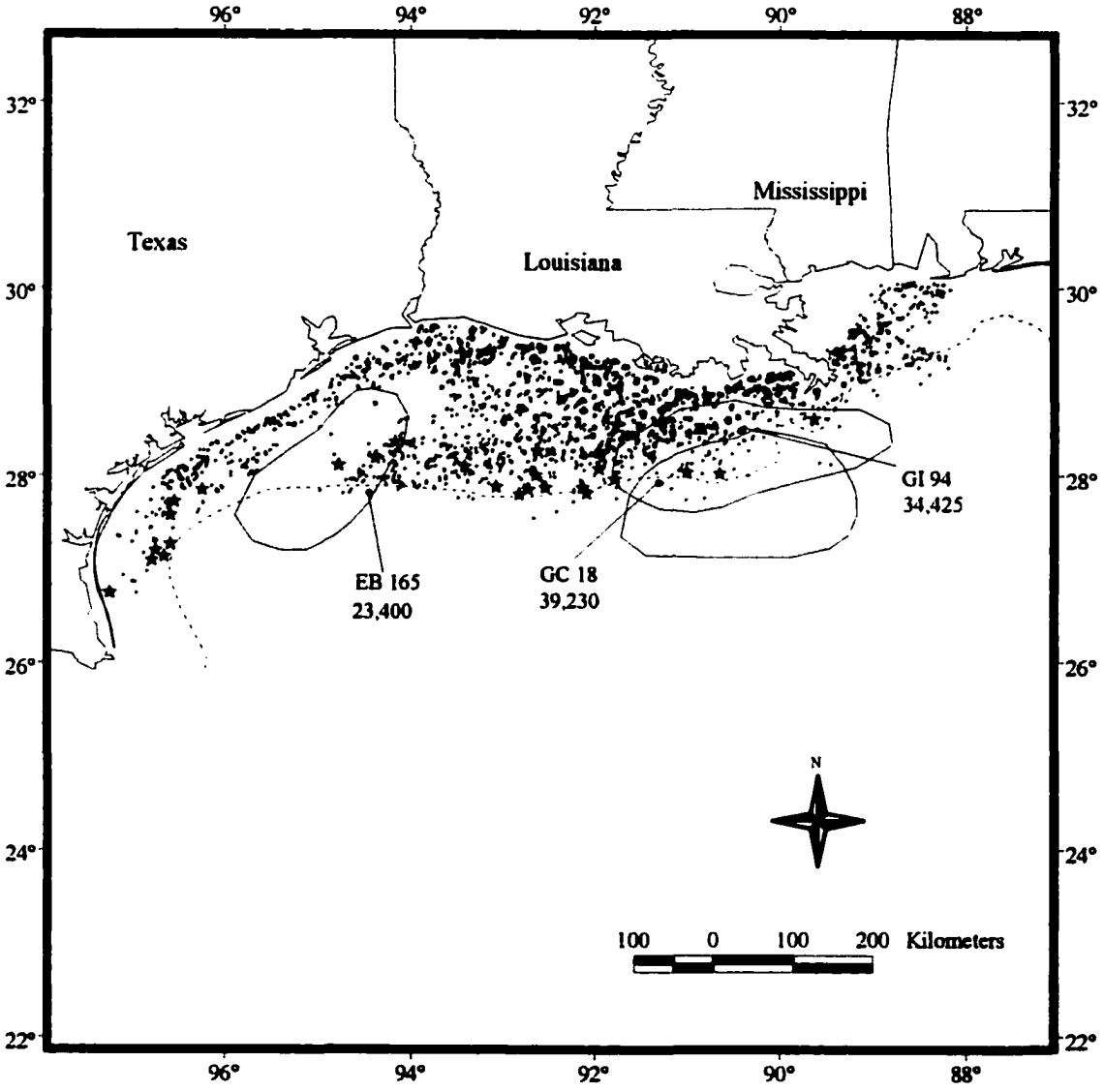


Figure 37. Seasonal transport polygons (including estimated spatial area in square km) for larvae arriving at the mid-shelf and shelf-break platforms, overlaid onto potential habitat sources (• = platform structures; ★ = natural reef sites) during the fall sampling period in 1996.

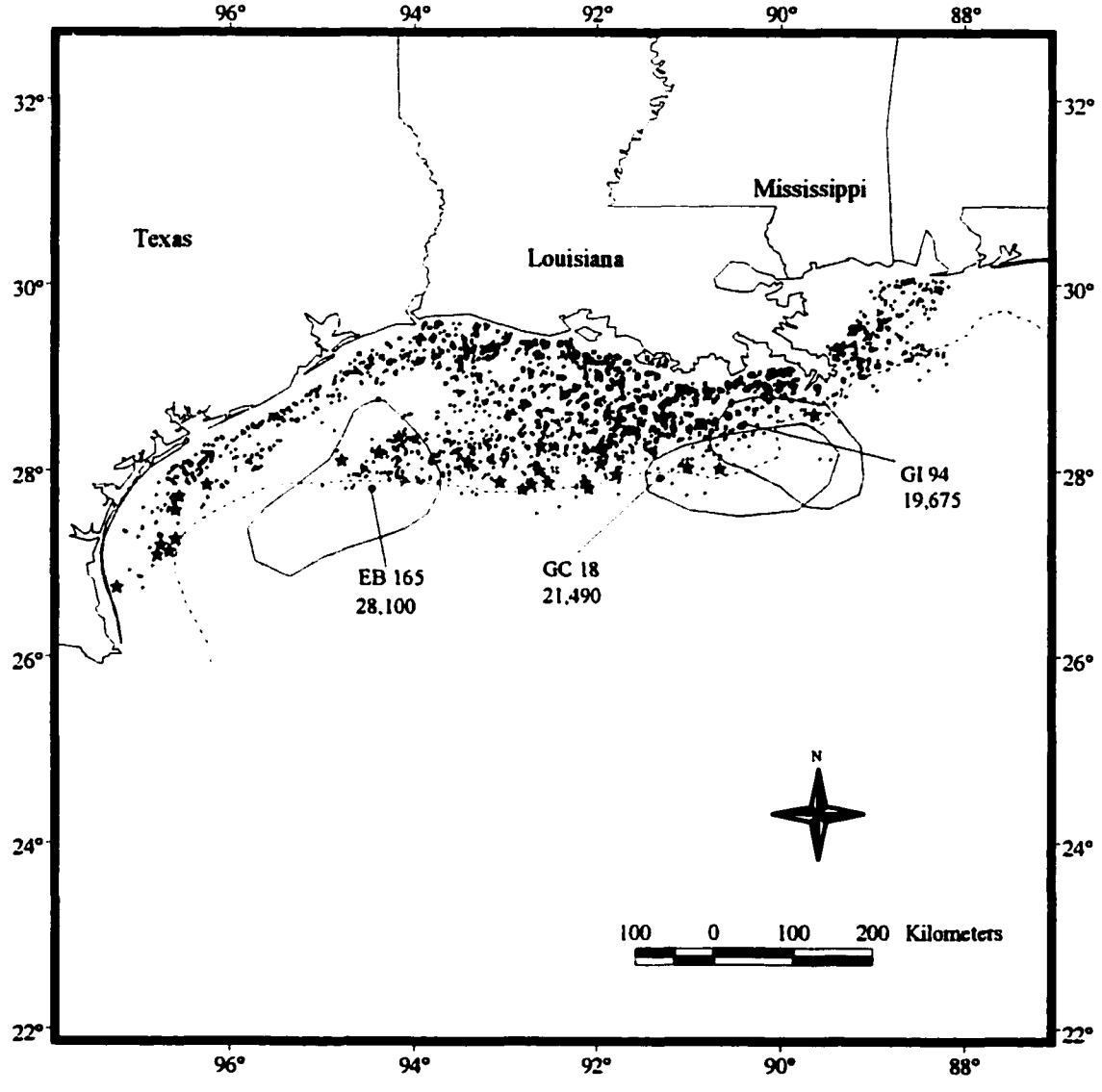


Figure 38. Seasonal transport polygons (including estimated spatial area in square km) for larvae arriving at the mid-shelf and shelf-break platforms, overlaid onto potential habitat sources (• = platform structures; ★ = natural reef sites) during the winter sampling period in 1996 and 1997.

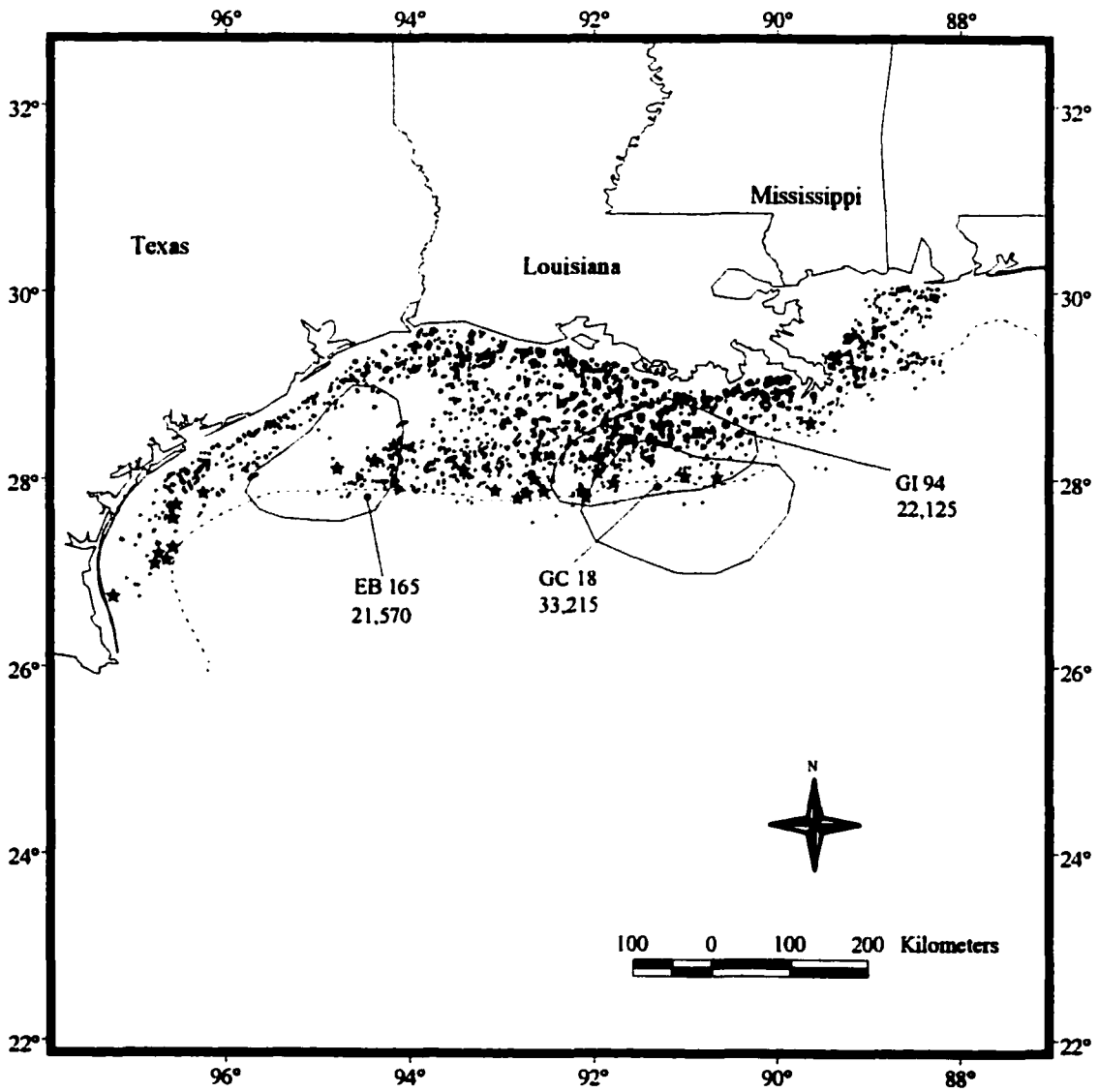


Figure 39. Seasonal transport polygons (including estimated spatial area in square km) for larvae arriving at the mid-shelf and shelf-break platforms, overlaid onto potential habitat sources (• = platform structures; ★ = natural reef sites) during the spring sampling period in 1997.

Table 14. Numbers of potential supply sources (both platforms and natural reef sites), identified from the TOPEX/POSEIDON and ERS-2 derived transport envelopes during seasonal sampling during 1996 and 1997.

	EB 165		GC 18		GI 94	
Season	Platforms	Reefs/Banks	Platforms	Reefs/Banks	Platforms	Reefs/Banks
Summer	59	1	123	10	652	2
Fall	62	3	37	2	386	3
Winter	114	3	38	2	112	1
Spring	94	3	90	5	783	11

platform (GI94) was generally to the northeast (mean angle = 55.5°), until a late summer flow reversal turned flow to the south (see Fig. 34). Although GI94 had ten times the number of potential source habitats than EB165 during the summer recruitment period (654 at GI94 vs. 60 at EB165), surface water collections at both locations were devoid of serranid larvae.

By the beginning of the fall season, the core of the Loop Current (at about 85° W longitude) began to pinch off its northern-most extent between 24° - 26° N and an anti-cyclone eddy feature formed (Fig. 40). This new formation was centered approximately 25° N and 87° W, and it continued to be closely associated with a CCR to its north until the following spring when it began moving west. After moving west of 88° W, this prominent CCR once again became associated with the progressing northern extent of the Loop Current. The western-most eddy formation (originally present west of 94° W at the beginning of the altimeter image series in late May) had moved south and dissipated off the southern Texas continental shelf. The eddy formation in the middle of the Gulf had moved farther west, resulting in a greater amount of disparity in the mean flow to the shelf-break platforms. Mean flow at EB165 was primarily to the south and east, resulting in the transport polygon encompassing similar numbers of potential source locations as compared to the summer. Flow at GC18 was directed to the north and west, with the largest transport polygon (39,320 km^2) encompassing the fewest numbers of source locations. The fall transport polygon surrounding GI94 was similar in size (34,424 km^2) to GC18, but

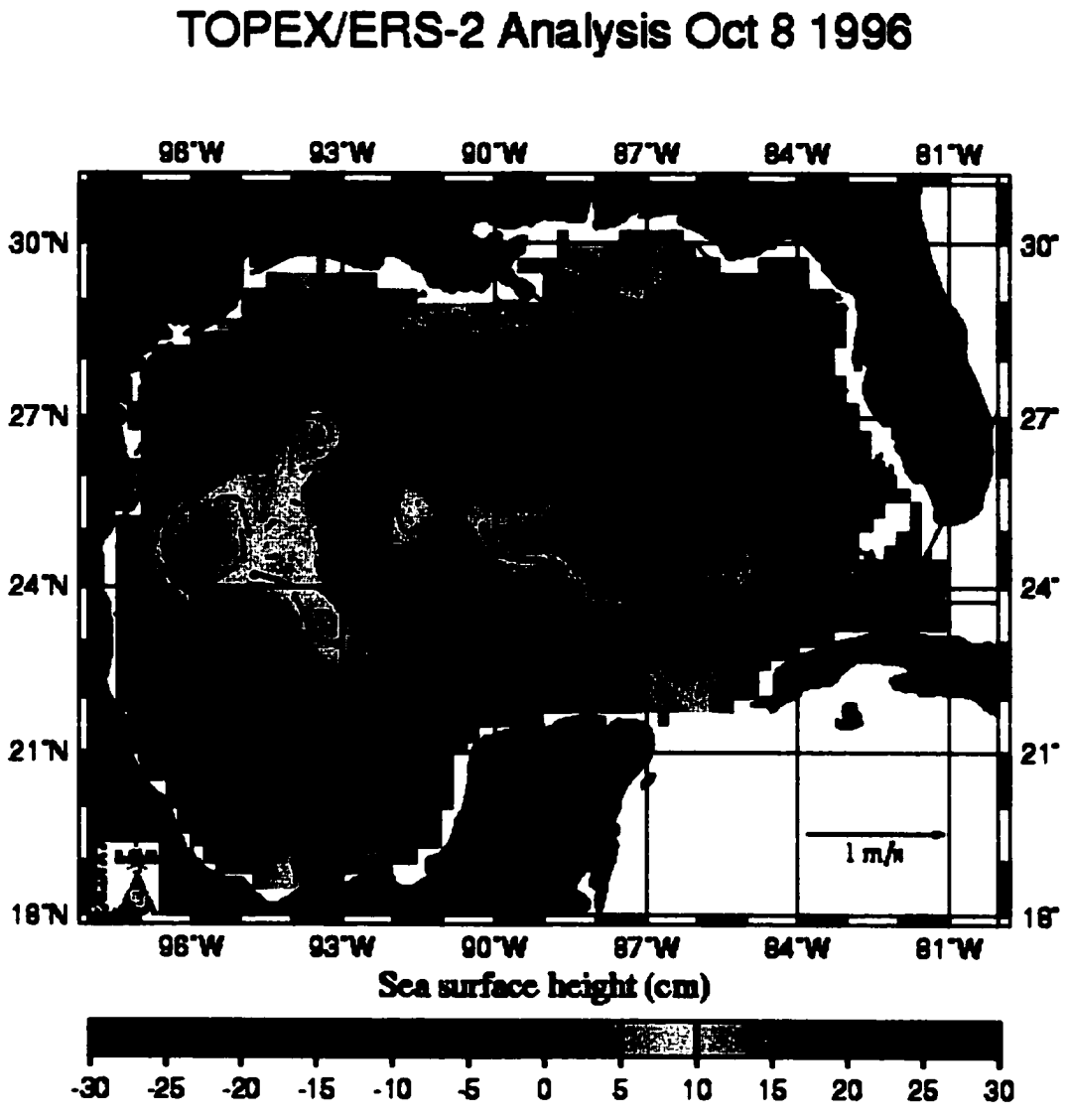


Figure 40. TOPEX/POSEIDON – ERS-2 plot of circulation in the Gulf identifying the leading edge of the Loop Current, as well as the newly formed eddy formation that was characteristic of the fall sampling period in 1996.

encompassed ten times the number of platform source locations. Reef-dependent larvae were more abundant at GC18 than GI94, where the transport envelopes showed that these two platforms could have supplied individuals to each other during the fall (see Fig. 37).

During winter, mean flow at both GC18 and GI94 was generally directed to the north and west, resulting in low numbers of potential source locations for both locations. Cold-core rings along the outer margin of the continental shelf helped influenced the geostrophic flow around these platforms (Fig. 41). The greatest amount of dispersion was seen at EB165 during winter (Table 13), resulting in the maximal seasonal spatial area for this platform (28,091 km^2). While the greatest number of potential source platforms for EB165 were within this seasonal polygon, the numbers of natural reefs/banks were similar to other seasons. During this season, the northern and western limits of the core of Loop Current were generally found below 25° N and east of 86° W.

The greatest numbers of serranid larvae were collected during the spring season, and mean flow in the spring of 1997 showed the greatest disparity between the two shelf-break stations. Mean flow at EB165 was generally south and east, whereas flow at GC18 was directed more north and west. Despite this apparent disparity in the direction of the current flow, the numbers of probable source locations were quite similar on each shelf-break platform during spring (94 platforms and 3 reefs/banks at EB165 vs. 90 platforms and 5 reefs/banks at GC18; see Table 14). Mean flow at GI94

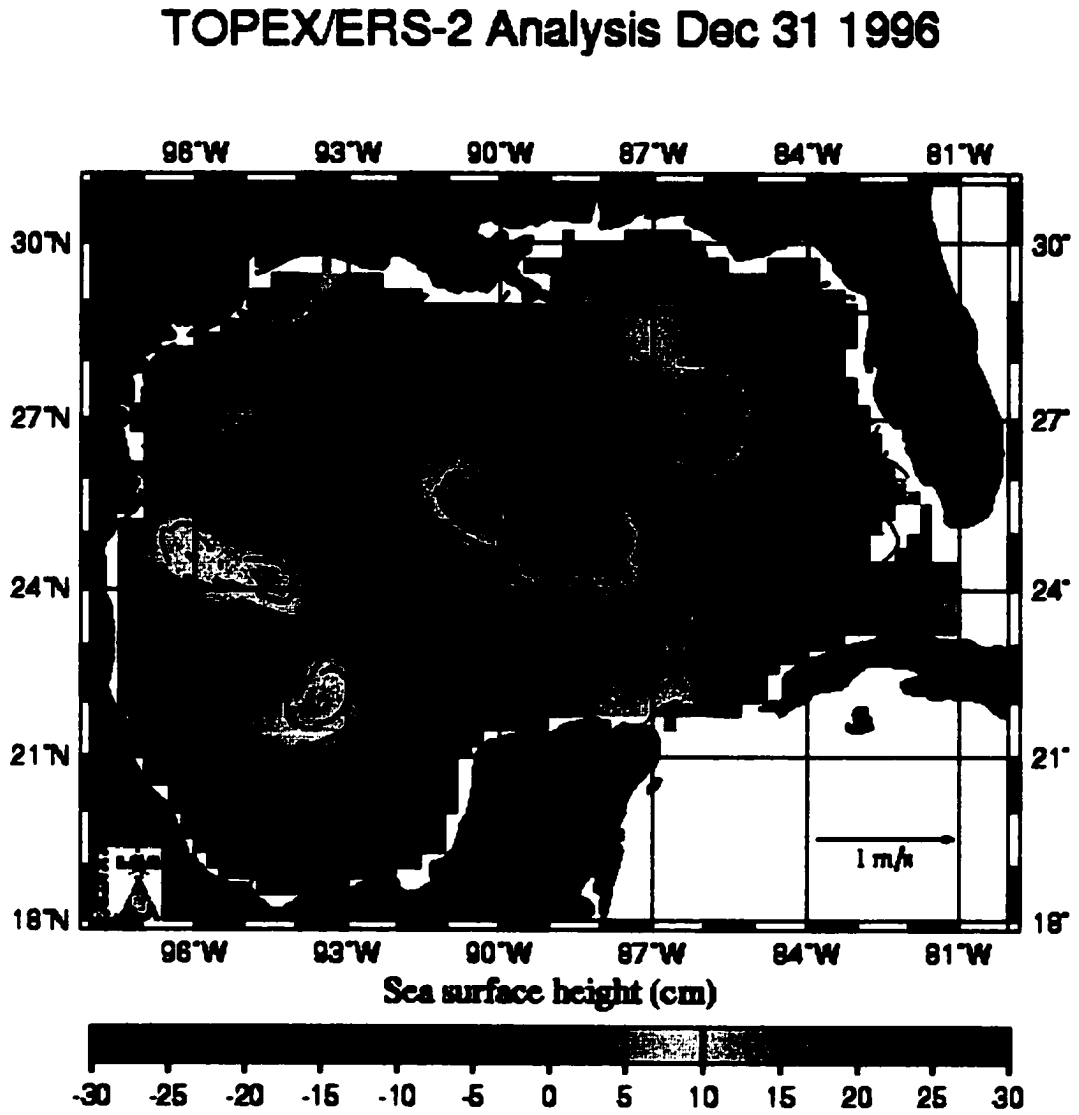


Figure 41. TOPEX/POSEIDON – ERS-2 plot of circulation in the Gulf of Mexico identifying to the prominent cold-core rings that were associated with the mesoscale eddies beyond the margin of the continental shelf during the winter sampling period in 1996 and 1997.

was more north and east, and the seasonal transport polygon encompassed the greatest numbers of potential source locations, both platforms and natural reefs/banks (Fig. 39).

Discussion

For this study, otolith-derived pelagic transport durations were used to determine the transit time in the plankton (from the time of fertilization to capture) for a representative family (Serranidae) of larval reef fishes in the northern Gulf. This back-calculation method provided a temporal measure from which I could estimate the spatial range of planktonic supply to platform habitats. Back-calculation methods are typically used to construct age-growth curves (Ralston 1976; Victor 1986b; Fowler 1989; Sponaugle and Cowen 1997), determine fertilization dates (Robertson 1988; Robertson et al. 1988), or document settlement dates (McFarland et al. 1985; Pitcher 1988; Tyler et al. 1993) for individual species. The present method was not directed at any individual species (the variable of interest was the mean age at capture for the entire serranid collection), and relied more on a representative age at capture relationship applied across different locations and environmental conditions (e.g., seasons). When paired with the physical transport information gained from the satellite altimetry, this technique provided a measure of the lateral distance that planktonic larvae could have been transported from the natal areas to the artificial reef platform habitats. While this technique cannot fully resolve neither the maximum nor minimum lateral transport distances, it can provide a relative measure (in terms of square kilometers of sea surface) of potential source areas.

Reef fish settle out of the plankton over a broad range of sizes (from < 4 mm SL to > 190 mm SL, Victor 1991a), yet there tends to be broad similarity in size at settlement within a given family (Victor 1991b). For 45 species of Pacific damselfishes, size at settlement ranged between 6 and 14 mm SL (Wellington and Victor 1989). The mean size of the serranids encountered during this study (< 4 mm SL; primarily at the shelf-break platforms) indicates that these individuals were predominantly in the presettlement planktonic stage. While size at settlement is somewhat narrowly defined within a family (the majority of reef-dependent families reportedly settle out of the plankton between 7 and 12 mm SL; Thresher et al. 1989; Thresher and Brothers 1989; Leis 1989), age at settlement is much more variable.

The determination of reef fish source areas (based on pelagic transport durations) relies on daily ring formation in the otoliths to infer spatial and temporal patterns of larval supply. While direct validation of daily ring formation is desirable, problems associated with obtaining live larvae and maintaining them in healthy conditions makes direct validation difficult (Crabtree et al. 1992). Given the general nature of daily increment formation in larval fishes (Panella 1971; Dean et al. 1983; Campana and Neilson 1985, Victor 1991a), assuming daily sagittal increments in the serranids seems warranted. Additional support for this assumption is provided by Keener et al. (1988), Doherty et al. (1994), and Colin et al. (1997), all of whom found daily ring formation in both larval and juvenile stage serranids (Epinephelinae, *Epinephelus striatus* and *Mycteroperca microlepis*; and Serraninae, *Plectropomus leopardus*). Although *Anthias nicholsi* (subfamily Anthiinae) comprised the vast

majority of the serranids collected during this study, they are morphologically most similar to the Serraninae in the larval stage (Baldwin 1990).

Few comparative studies are available to document the larval durations for most serranid larvae, with only a few epinephelines having been previously investigated. Settlement size for *Epinephelus* spp. has been reported to be about 25 mm SL, and the time to reach this stage varies from 35 to 50 days (Leis 1987). Similar larval durations have been reported for *Mycteroperca microlepis* and *M. bonaci* (mean larval duration = 43 and 41 days respectively, Keener et al. 1988). Maximum larval durations as high as 45 days for *Epinephelus striatus* around Exuma Sound were estimated by Colin et al. (1997), although they noted that this may not represent the absolute maximum because late-stage pelagic larvae likely encountered favorable settlement and circulation conditions around the Sound. None of the presettlement stage epinephelid larvae collected during this study were approaching these elevated larval durations, indicating that for this serranid subfamily, spawning-supply linkage distances to platform habitats were not directed primarily by long-range transport mechanisms.

Based on the one-year series of altimeter images, at no time during the sampling period of 1996 or 1997 did the northern boundary of the Loop Current progress far enough north and west to directly impact the study platforms in the central region of the Gulf (either GC18 or GI94). This is not to say, however, that the Loop Current does not directly impact reef-fish recruitment. The characteristics of the anticyclonic eddies periodically shed from the Loop Current are a direct reflection of both the physical (temperature, nutrients, dissolved oxygen, etc.) and biological (zooplankton

abundance, ichthyoplankton abundance and diversity, etc.) characters of the Loop Current interior. Once shed, these eddies move west at about 2 km/day (Elliot 1982) and could potentially transport recruits into the general location of both artificial reefs and natural reef banks within the central Gulf of Mexico.

The altimeter-derived transport envelopes over the Texas-Louisiana shelf matched reasonably well the wind-driven circulation patterns presented by both Merrell and Morrison (1981) and Cochrane and Kelley (1986). The prominent eastward flow during summer near the continental shelf-break corresponded to the southern limit of the Texas-Louisiana shelf cyclonic gyre. Despite numerous source locations within each transport polygon during summer (Fig. 36, EB165 and GI94), few reef-dependent larvae and no serranid larvae were collected from either platform during this season. Similarly, the number of potential artificial reef sites supplying GC18 in the fall was an order of magnitude less than GI94 (37 potential sites at GC18 vs. 386 sites for GI94), yet similar numbers of serranids were collected from both locations. Therefore, simple increases in the numbers of potential source areas (e.g., artificial reef platforms) alone may not be a good predictor of larval reef fish abundance in the plankton.

The dominance of the anthiinid serranids at the shelf-break platforms reinforces the zoogeographical patterns of serranids proposed by G.B. Smith (1976), where adult *Anthias nicholsi*, *A. woodsi*, and *Hemanthias vivamus* were taken mainly from depths ranging from 73-427 m (similar water depths as the shelf-break stations). Increased abundance of anthiinids from offshore stations in the eastern Gulf, primarily *H. vivanus* from waters > 100 m, were also noted by Houde (1982). Many other serranids occur

in the eastern Gulf at much greater depths than they occupy in more tropical waters (Courtenay 1967), with accounts of offshore occurrences from depths > 30 m being common. Adult members of the epinephelids (*Epinephelus adscensionis*, *Mycteroperca phenax*, and *M. microlepis*) and grammistinids (*Rypticus maculatus* and *R. bistrispinus*) were commonly encountered at depths > 30 m on the mid-shelf and shelf-break platforms, but were represented in the plankton by only a few individuals collected over a single season. Oddly, the most numerically abundant adult serranid found on any of the study platforms (*Paranthias furcifer*) was represented by only five larvae collected over the entire course of this study. Similarly, *P. furcifer* was completely absent from the > 5,300 serranid larvae collected in the eastern Gulf by Houde (1982).

The seasonally averaged 14.5-day transport envelopes reflected a general pattern of reef fish supply to platforms coming from W of 90° W latitude. The cold-core ring, in close association with westerly migrating warm-core eddies, provided much of the directionality to the surface flow potentially determining reef fish transport. Numerically, other artificial reef structures (= platforms) were the most probable source locations for reef fish recruitment to the mid-shelf and shelf-break study platforms.

CHAPTER 3: COMPARISONS OF REEF DEPENDENT FISH COMMUNITIES ON "ARTIFICIAL REEF" PLATFORMS TO RESIDENT POPULATIONS ON NATURAL REEF SITES

Introduction

To better understand how larval dispersal influences the replenishment of open marine populations, some fisheries biologists have recently focused on the central ideas surrounding the 'source and sink' theories of population dynamics (Pulliam 1988; Fairweather 1991; Roberts 1997). Areas that contribute disproportionately large quantities of offspring to future generations are known as sources, and those that provide relatively few, but still support populations, are known as sinks (Lawton 1993; Roberts 1998). The establishment of marine reserves (either natural or artificial reef areas designated as "limited harvest" to "no-take zones") at the appropriate spatial scales within source areas is thought to be an effective means of maintaining populations and preserving genetic diversity (Carr and Reed 1993; Nowlis and Roberts 1998).

Larval export to distant non-reserve areas (Bohnsack 1990; Man et al. 1995; Holland and Brazee 1996) as well as adult spillover to nearby habitats and fishing grounds (Polachek 1990; DeMartini 1993; Rakitin and Kramer 1996; Russ and Alcala 1996) are just two examples of reserve-induced fisheries enhancements that ultimately help to decrease the probability of stock collapses. In overfished stocks, marine reserves can also accelerate recoveries, provided the reserves themselves are located within areas characterized by having substantial upstream sources (Roberts 1995).

Proponents of artificial reef programs have seized upon the positive aspects of the source and sink theory (fisheries accumulation in sink areas) in their efforts to enhance local coastal fisheries (reviewed in Bohnsack and Sutherland 1985; but also see Alevizon and Gorham 1989; Baqueiro and Mandez 1994; Bohnsack et al. 1994; Bortone et al. 1994; Cummings 1994). Both Texas and Louisiana have active programs to convert existing platform structures into artificial reef sites (Wilson et al. 1987; Bull and Kendall 1994). Opinions regarding the ecological function of artificial reefs remains divided in terms of whether they serve to aggregate naturally-dispersed stocks (Ambrose and Swarbrick 1989), or their presence allows for measurable increases in stock biomass by enhancing production (Polovina and Sakai 1989; Bohnsack et al. 1994; Bohnsack 1996).

Artificial reefs can increase exploitable biomass either by increasing total biomass or concentrating available biomass, as long as recruitment overfishing does not occur (Polovina 1991). When overfishing does occur, artificial reefs can magnify overfishing pressures by aggregating remaining fishes, thus making them even more vulnerable to harvest. Increased fish production is most likely where reef habitat is limiting, when fishing effort is low, and when a large stock reservoir exists relative to harvest (Bohnsack 1989). Artificial reefs are unlikely to increase total productivity in highly mobile species, heavily fished species, or species that settle in non-reef habitats (Stone 1985; Mapstone and Fowler 1989; Brock and Kam 1994). The ultimate functional role of the platform "artificial reefs" is still yet to be fully resolved.

The objective of this study was to compare the reef-dependent fish communities found on platform artificial reefs (presumed sinks) to the resident reef fish populations found on nearby natural reef sites (presumed sources). Specific questions asked to achieve these objectives were: (1) are consistent reef-dependent fish assemblages present on natural and artificial reef sites in the northern Gulf of Mexico (Gulf), and (2) what is the relationship between reef-dependent fish composition and the physical characteristics of the reef habitats?

Methods and Materials

Ichthyofaunal surveys of natural reef and hard-bottom communities were performed by the Southeast Area Monitoring and Assessment Program (SEAMAP), National Marine Fisheries Service, Pascagoula, MS. Fish trap/video reef fish surveys (Gledhill et al. 1996) have been used to document the relative abundance of reef fishes in the northern Gulf from Texas to Florida. Video records collected from the 1994 and 1995 cruises were used in this study to compare reef-fish communities recorded from 16 natural reef/hard-bottom sites on the continental shelf with those found at the mid-shelf and shelf-break study platforms (Fig. 42).

At each study platform (GI94, GC18, and EB165), juvenile and adult reef-dependent fish communities were surveyed during 1994 – 1997 with either scuba divers or a remotely operated vehicle (ROV). Point-count diver surveys (Thresher 1984; Bohnsack and Bannerot 1986) were limited to the upper 50 m (maximum depth for point-count survey at GC18 and GI94 = 30 m), whereas ROV surveys collected data

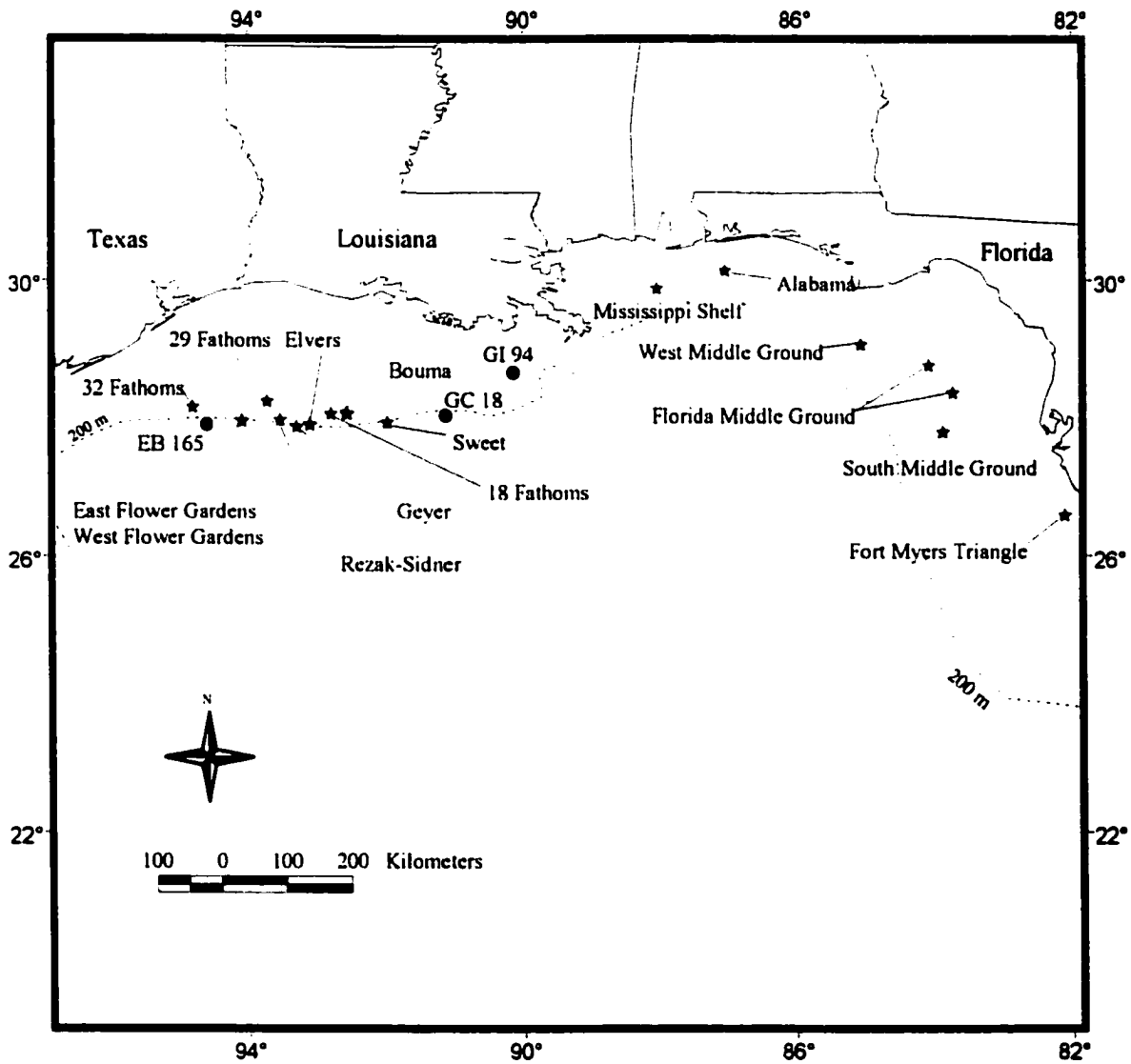


Figure 42. Locations of the 16 natural reef sites (★) sampled by National Marine Fisheries Service SEAMAP fish trap/video deployments during 1994 and 1995, and platform locations (•) sampled during 1994 – 1997 for this study.

from the surface to >150 m depth at GC18 and to the seafloor GI94 (61 m depth). Species abundance data were standardized to 1-hour intervals, and abundance estimates for all reef-dependent taxa were determined by the following discrete scale: 0 = absent; 1 = rare (1-5 individuals / hour); 2 = uncommon (5-20 individuals / hour), 3 = common (20-100 individuals / hour), and 4 = numerous (> 100 individuals / hour).

SEAMAP videotapes were viewed in the laboratory with a video tape player and television monitor with capabilities for freeze-frame, variable slow motion, double-speed viewing, and forward and reverse search modes with picture. Double-speed viewing was used over habitats with very low fish densities. High fish densities often necessitated short segments of tape being reversed and reviewed up to 10 separate times in order to record all fishes present within the viewing area. Tape analysis consisted of viewing one continuous hour of reef-site video and tabulating the total numbers of all fishes in view. Fishes were identified to the lowest possible taxon. The SEAMAP Project Leader and other NMFS biologists confirmed all identifications.

Physical characteristics of each natural reef site are presented in Appendix C. Readers estimated rugosity of each reef habitat (including maximum vertical relief and average vertical relief, in meters) directly from the tapes. Dominant relief types (both biotic and abiotic characteristics) were also recorded. Water depths were taken from ships log. Reef-dependent species (all taxa within the reef-dependent functional group determined for this study) were later extracted from the larger SEAMAP data set and their scaled abundance values determined (discrete scale, 0 – 4). When multiple video

samples were collected from a single reef site, the maximal abundance value for each taxon was used for analysis.

Statistical Analysis

Fish assemblages (groups of stations with similar species compositions) were determined by cluster analysis of the species-station matrices (rows = species, columns = stations). Matrix entries were the standardized abundance values noted for each species/station combination. Hierarchical agglomerative cluster analysis using complete linkage sorting strategy (SYSTAT 1992) based on Bray-Curtis similarities (Bray and Curtis 1957). This analysis identifies "natural groupings" of samples such that samples within a group are more similar to each other than to samples in different groups (Clarke and Warwick 1994). Complete linkage sorting ensures that all items in a cluster are within some maximum distance (or minimum similarity) of each other (Johnson and Wichern 1992). When it can be established that stations (artificial reef platforms, natural reef areas, hard bottom banks, etc.) can be distinguished from one another, stations can be partitioned into groups with similar community structure. In the dendrogram, I graphically delineated reef-dependent fish assemblages by grouping stations that contained a minimum of 20% similar species composition.

The Bray-Curtis coefficient (S_{jk}), or the similarity between the *j*th and *k*th stations, has the following definition:

$$S_{jk}(i) = 100 \times \left[1 - \frac{\Sigma |y_{ij} - y_{ik}|}{\Sigma (y_{ij} + y_{ik})}\right] \quad \text{summed from } i = 1 \text{ to } p, \qquad (1)$$

where y_{ij} represents the abundance of species y the *i*th row and *j*th column of the data matrix, and *p* is *p*th element in the species list. In the Bray-Curtis measure, S = 0 if the two stations have no species in common, and S = 1 if the community composition is identical, since $|y_{ij} - y_{ik}| = 0$ for all *i*. The Bray-Curtis measure was adopted because it is not effected by joint absences, and is sufficiently robust for marine survey data where many species are absent from the majority of samples (Field et al. 1982).

The contribution of each individual species (*i*) to the observed fish assemblages was calculated by similarity percentage analysis (SIMPER, Clarke and Warwick 1994). Values of S_{jk} (*i*) were then averaged over all pairs of stations $_{(j,\,k)}$ between fish assemblages to give the average contribution, $Savg_{(i)}$, of the i^{th} species to the total similarity between the compared assemblages. The ratio of $Savg_{(i)}$ to its standard deviation, $Savg_{(i)}/SD(S_{(i)})$, indicates how consistently a species discriminates among the assemblages. If a species is found at consistent levels throughout an assemblage, then the standard deviation of its contribution is low, and the ratio is high (Clarke and Warwick 1994). Such a species will contribute more to the intra-group similarity, and can be though of as typifying that group.

Analogously, the average contribution from the i^{th} species to the overall dissimilarity (δ_{jk} (*i*) = 1 – S_{jk} (*i*), see equation (1)) between groups was determined, and each average contribution, $\delta avg_{(i)}$, and ratio, $\delta avg_{(i)}/SD(\delta_{(i)})$ calculated. Species with large ratio values not only contribute greatly to the measured dissimilarity between groups, but also do so consistently across all inter-comparisons of samples between groups. These similarity percentages provide a useful measure to assess how

consistently a species is encountered within the identified clusters, thereby determining the best "discriminating" species among the groups.

The Bray-Curtis dissimilarity matrix (δ_{jk} (i) values from the SIMPER analysis) was also used as input for a non-metric multidimensional scaling (MDS) analysis of the 19 stations (16 natural reef sites and three artificial reef platforms). MDS seeks to compute coordinates for a set of points in a unit-less space such that the distances between pairs of point's fit as closely as possible to measured dissimilarity between a corresponding set of objects (SYSTAT 1992). A non-metric MDS performs this by fitting a monotonic (increasing) regression of the interpoint distances to the dissimilarity measure, with the only information used from the dissimilarity measure being the rank order (Shepard 1962; Kruskal 1964; Johnson and Wichern 1992). Stress, or the "goodness-of-fit" of this regression, varies from 0 to 1 with values nearer 0 indicating a better fit.

MDS was first performed in three dimensions, and this configuration was then used as a starting point for the two-dimensional MDS. Numerous iterations were carried out in order to ensure the global minimum and not a local minimum was reached upon convergence. Final configurations (in both two and three dimensions) were further assessed with (Zar 1984) diagrams to detect the locations that were least adequately represented by an n - D configuration. The main advantage of MDS over other ordination techniques (principle co-ordinates, reciprocal averaging, etc.) is that MDS is not based on an eigenvalue extraction of principle components, a method

relatively inflexible with regard to the large number of zero counts generally present in a species-sample matrix (Field et al. 1982).

Results

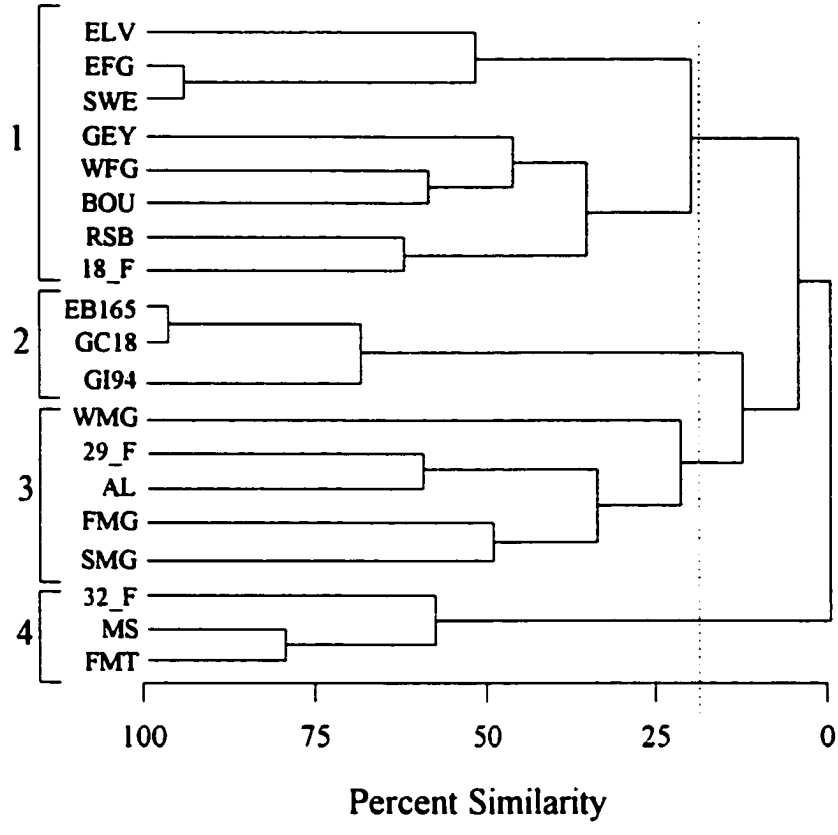
SEAMAP video sampling consisted of 118 deployments of the fish trap/video unit on 16 natural reef sites, resulting in 105 hours of video footage. A total of 41,190 individuals from the seven reef-dependent families were enumerated (Table 15). Bray-Curtis complete linkage clustering revealed that at a 20 % similarity level, a general west-east separation of four primary groups were identified (Fig. 43). All sites within Group 1 were located west of 90° W longitude, and all but two sites (29-Fathom and 32-Fathom Banks) in Groups 3 and 4 were located east of 90° W. The artificial reef platforms (Group 2, all west of 90° W) clustered most similarly amongst themselves, but were more similar in reef-fish community composition to the eastern Gulf sites (Group 3) than to the geographically-closer, natural reef sites found on the Texas and Louisiana shelf (Group 1). The low diversity sites of Group 4 (Mississippi Shelf (MS), Fort Myers Triangle (FMT), and 32-Fathom Bank) were the least similar and generally corresponded to stations containing only one or two reef-dependent taxa. The cohesiveness of the natural reef sites (i.e., the internal biological similarity within Groups 1, 3, and 4) are about equal, with the exception of Group 1, where Sweet Bank (SWE) and East Flower Garden (EFG) are connected highest on the dendrogram (Fig. 43). The artificial reef platforms located farthest offshore (GC18 and EB165) clustered highest on the dendrogram (% similarity = 97).

Table 15. Most abundant (top 90%) reef-dependent species enumerated from the SEAMAP fish trap/video deployments in the northern Gulf of Mexico during 1994 and 1995. Frequncy (Freq.) equals the total number of stations each taxa was encountered. Number equals total number of individuals enumerated in the SEAMAP survey.

Taxa	Freq.	Number	Taxa	Freq.	Number
Serranidae	13	221	Pomacanthidae (cont.)		
Centropristis ocyurus	1	16	*H. ciliaris*	5	62
Diplectrum formosum	6	52	*H. tricolor*	5	36
Epinephelus adscensionis	6	51	*Pomacanthus Arcuatus*	1	5
E. cruentatus	3	76	*P. paru*	7	18
E. guttatus	2	2			
E. morio	3	44	Pomacentridae		
Hypoplectrus unicolor	2	48	*Abudefduf Saxatilis*	3	1425
Liopropoma eukrines	8	101	*Chromis cyaneus*	6	1725
Mycteroperca interstitialis	7	143	*C. enchrysurus*	11	8913
M. microlepis	6	12	*C. insolatus*	2	422
M. phenax	14	181	*C. multilineatus*	4	195
Paranthias furcifer	11	16020	*C. scotti*	4	142
Pronotogrammus martinicensis	9	3389	*Pomacentrus fuscus*	3	155
Rypticus maculatus	4	38	*P. leucosticus*	5	30
Serranus annularis	6	147	*P. partitus*	6	822
S. pheobe	10	194	*P. planifrons*	4	105
			P. variabilis	4	472
Chaetodontidae					
Chaetodon aculeatus	3	18	Labridae	15	984
C. aya	7	67	*Bodianus pulchellus*	11	255
C. ocellatus	10	47	*B. rufus*	4	15
C. sedentarius	14	327	*Decodon puellaris*	6	237
			Halichoeres Bathyphilus	5	370
Pomacanthidae			*H. bivittatus*	6	1004
Centropyge argi	10	804	*H. garnoti*	2	9
Holocanthus bermudensis	9	374	*H. maculipinna*	1	69

Table 15 (cont.)

Taxa	Freq.	Number	Taxa	Freq.	Number
Labridae (cont.)			Scaridae (cont.)		
H. pictus	3	24	*Sparisoma aurofrenatum*	5	58
H. poeyi	3	5	*S. rubripinne*	0	0
Thalassoma bifasciatum	6	194	*S. viride*	5	25
Scaridae	6	255	Acanthuridae		
Scarus croicensis	3	366	*Acanthurus chirurgus*	5	208
S. taeniopterus	3	5	*A. coeruleus*	6	187
S. vetula	4	21			
			Total Individuals		41,190



Group 1 - ELV = Elvers Bank, EFG = East Flower Garden, SWE = Sweet Bank
GEY = Geyers Bank, WFG = West Flower Garden, BOU = Bouma Bank
RSB = Rezak-Sidner Bank, 18_F = 18 Fathom Reef

Group 2 - EB165, GC18, GI94

Group 3 - WMG = West Middle Grounds, 29_F = 29 Fathom Reef, AL = Alamaba Shelf
FMG = Florida Middle Grounds, SMG = South Middle Grounds

Group 4 - 32_F = 32 Fathom Reef, MS = Mississippi Shelf, FMT = Fort Myers Triangle

Figure 43. Cluster dendrogram showing the percent similarity among 19 hard-bottom communities in the northern Gulf of Mexico. Similarity matrix based on Bray-Curtis measure, and the dendrogram formed by complete linkage sorting. Four main station groups (1-4) are distinguished by the dotted line at an arbitrary similarity level of 20% (X-axis).

For the similarity percentage analysis (SIMPER), Group 4 was excluded due to low numbers of reef-dependent species encountered at each site within this cluster. For example, at Fort Myers Triangle (FMT) and the Mississippi Shelf (MS) sites, only *Diplectrum formosum* (average abundance = 2.8 and 2.1, respectively) was noted, whereas at 32-Fathom Bank, *D. formosum* (average abundance = 2.2) and *Serranus phoebe* (average abundance = 1.3) were the only species seen. Although few reef-dependent species were noted from 32-Fathom Bank, numerous reef-associated families were well represented (e.g., Carangidae: *Seriola dumerili*; Lutjanidae: *Lutjanus campechanus* and *Rhomboplites aurorubens*; Mullidae: *Upeneus parvus*; and Tetraodontidae: *Lagochephalus laevigatus*). Similar diversity of reef-associated families was not encountered at either FMT or MS.

The reef-dependent taxa accounting for the overall similarity within the station groupings are listed in Table 16. Over one-half of average percent similarity within the western Gulf sites of Group 1 is contributed by five taxa; *Pronotogrammus martinicensis* (= *Holanthias martinicensis* as determined by Olmi [1986]), Labridae (primarily the deep-dwelling species *Decodon puellaris* and *Halichoeres bathyphilus*), *Chromis enchrysurus*, and *Paranthias furcifer*, with the first two being found at very consistent levels within the group (largest ratio values, $Savg_{(i)}/SD(S_{(i)})$, of 1.72 and 1.40, respectively). *Paranthias furcifer* were also found at consistent levels within this group (mean abundance = 2.50, ratio = 1.28).

Table 16. Mean abundance (discrete abundance scale) and average percent similarity (SIMPER, within assemblage) of the fish assemblages defined by Bray-Curtis similarity cluster analysis. Nomenclature follows that of Robins et al. (1991).

	Assemblage		
Taxa	Group 1	Group 2	Group 3
Serranidae			
Diplectrum formosum	0.00	0.00	0.40
Epinephalus adscensionis	0.00	1.33	0.00
E. guttatus	0.00	0.67	0.00
E. morio	0.00	0.00	1.00
Hypoplectrus unicolor	0.00	0.00	0.80
Liopropoma eukrines	1.13	1.33	0.60
Mycteroperca interstitialis	0.75	0.00	1.60
M. microlepis	0.50	0.67	0.00
M. phenax	1.75	1.00	1.80
Paranthias furcifer	2.50	3.67	0.00
Pronotogrammus martinicensis	3.63	0.00	0.00
Rypticus maculatus	0.00	1.67	0.00
Serranus annularis	1.38	0.00	0.00
S. pheobe	1.25	0.00	2.00
Chaetodontidae			
Chaetodon aculeatus	0.38	0.00	0.00
C. aya	1.00	0.00	0.60
C. ocellatus	0.00	1.00	1.60
C. sedentarius	1.75	2.00	2.20
Pomacanthidae			
Centropyge argi	1.75	2.33	0.00
Holocanthus bermudensis	0.25	1.00	2.40
H. ciliaris	0.00	0.67	0.60
H. tricolor	0.25	1.67	0.00
Pomacanthus paru	0.25	1.67	0.00
Pomacentridae			
Abudefduf saxatilis	0.00	4.00	0.00
Chromis cyanea	0.00	2.33	0.00

Table 16. (cont.)

Taxa	Assemblage		
	Group 1	Group 2	Group 3
Pomacentridae (cont.)			
C. enchrysurus	2.75	0.00	3.20
C. insolata	0.00	0.00	2.00
C. multilineata	0.00	1.67	0.00
C. scotti	1.00	0.00	0.00
Microspathodon chrysurus	0.00	1.00	0.00
Pomacentrus fuscus	0.00	2.00	0.00
P. luecostictus	0.00	1.33	0.60
P. partitus	0.00	3.67	1.60
P. planifrons	0.00	1.33	0.00
P. variabilis	0.00	2.00	0.00
Labridae	2.50	2.00	2.60
Bodianus pulchellus	1.50	2.67	1.00
B. rufus	0.00	1.00	0.00
Decodon puellaris	2.00	0.00	0.00
Halichoeres bathyphilus	1.75	0.00	0.00
H. bivittatus	0.75	0.00	2.00
H. poeyi	0.25	0.00	0.00
Thallasoma bifasciatum	0.00	3.67	1.33
Scaridae	0.00	1.67	1.00
Sparisoma aurofrenatum	0.00	2.00	0.00
S. rubripinne	0.00	1.00	0.00
S. viride	0.00	1.00	0.00
Acanthuridae			
Acanthurus coeruleus	0.00	2.33	0.60
Average percent similarity (S_i)	44.29	79.94	37.78

The artificial reef platforms of Group 2 had the highest average percent similarity and the greatest number of co-occurring species found within any cluster (20 co-occurring species for Group 2 vs. 9 each for Groups 1 and 3). Each of the seven reef-dependent families are well represented, with very high abundance of *Abudefduf saxatilis*, *Thalassoma bifasciatum*, *Paranthias furcifer*, and *Pomacentrus partitus* (mean abundance > 3.5 for each species). Although *Acanthurus coeruleus* had a high mean abundance and contributed the second highest amount to the overall similarity, it had a relatively low ratio value (not found at consistent levels) when compared to the other taxa within Group 2.

The eastern Gulf sites of Group 3 had the lowest average similarity, with five taxa (*Chromis enchrysurus*, *Serranus phoebe*, *Holocanthus bermudensis*, small unidentified Labridae, and *Chaetodon ocellatus*) accounting for greater than 50 % of the overall similarity. While contributing only a small amount to the overall similarity, *Mycteroperca phenax* was found at consistent levels across all samples within this group (mean abundance = 1.80, ratio = 2.30). Eastern Gulf sites were characterized by mid-depth serranids (*Serranus phoebe* and *Mycteroperca phenax*), chaeotodontids (*Chaetodon ocellatus* and *C. sedentarius*), and pomacanthids (*Holocanthus bermudensis*).

Average contributions of each taxa accounting for the dissimilarity among Groups 1, 2, and 3 are shown in Table 17. Nearly 52% of the average dissimilarity between the platform artificial reefs of Group 2 and the western Gulf sites of Group 1

Table 17. Comparisons of selected taxa within fish assemblages identified from Groups 1, 2, & 3 based on total contributions to the average dissimilarity between Groups. The percent contribution (%) to the average dissimilarity between compared assemblages and the ratio of the average contribution, $\delta avg_{(i)}/SD(\delta_{(i)})$, are listed. Taxa with largest ratio values are identified in bold. A dashed line represents no taxa contribution to the comparison.

Taxa	Group 2 vs. 1		Group 2 vs. 3		Group 3 vs. 1	
	%	Ratio	%	Ratio	%	Ratio
Serranidae						
Epinephelus adscensionis	1.87	3.05	1.68	2.06	-	-
E. morio	-	-	-	-	1.95	1.06
Liopropoma eukrines	-	-	1.49	1.53	1.54	1.01
Mycteroperca interstitialis	-	-	2.22	1.32	3.53	1.16
M. microlepis	-	-	-	-	1.37	0.73
M. phenax	1.69	1.78	-	-	2.88	0.95
Paranthias furcifer	2.32	1.10	4.67	**3.87**	4.51	**1.45**
Pronotogrammus martinicensis	5.07	2.64	-	-	6.57	**1.30**
Rypticus maculatus	2.24	**4.06**	2.20	3.51	-	-
Serranus annularis	1.72	0.94	-	-	2.68	0.92
S. pheobe	-	-	2.66	2.74	3.29	**1.46**
Chaetodontidae						
Chaetodon sedentarius	-	-	1.47	1.15	3.27	1.13
C. ocellatus	-	-	-	-	2.28	**1.46**
Pomacanthidae						
Centropyge argi	2.64	1.10	2.83	1.35	3.45	0.98
Pomacanthus paru	1.98	2.16	1.85	1.92	-	-
Holocanthus tricolor	1.98	2.16	2.20	3.51	-	-
H. bermudensis	-	-	1.62	1.16	4.17	**1.78**
Pomacentridae						
Abudefduf saxatilis	5.61	**4.16**	5.51	**3.60**	-	-
Chromis cyanea	3.03	2.63	3.17	**3.52**	-	-
C. enchrysurus	3.61	1.52	4.06	1.72	3.88	0.79
C. insolata	-	-	2.40	1.15	3.62	1.10
C. multilineata	2.12	2.76	2.20	3.51	-	-

Table 17 (cont.) Taxa	Group 2 vs. 1 %	 Ratio	Group 2 vs. 3 %	 Ratio	Group 3 vs. 1 %	 Ratio
Pomacentridae (cont.)						
Pomacentrus luecostictus	1.82	2.91	1.41	1.45	-	-
P. partitus	5.05	**5.62**	3.52	1.31	2.58	0.73
P. variabilis	2.81	**4.16**	2.75	**3.60**	-	
Labridae	1.80	1.23	2.04	1.50	3.20	1.11
Bodianus pulchellus	2.12	1.17	2.16	1.43	2.83	1.13
Decodon puellaris	2.81	1.11	-	-	4.32	0.99
Halichoeres bathyphilus	2.41	0.96	-	-	3.76	0.96
H. bivittatus	-	-	2.35	1.06	3.62	1.13
Thalassoma bifasciatum	4.80	**3.38**	4.61	2.61	-	-
Scaridae	2.21	**3.56**	2.33	**4.25**	1.27	0.62
Sparisoma aurofrenatum	2.48	1.35	2.39	1.25	-	-
Acanthuridae						
Acanthurus coeruleus	4.95	2.53	4.48	2.00	-	-
Total percent dissimilarity	77.12		74.73		69.38	

was accounted for by 14 taxa, with four (*Abudefduf saxatilis*, *Pomacentrus partitus*, *Thalassoma bifasciatum*, and *Pomacentrus variabilis*) identified as "discriminating". Each of these four were found at consistently higher abundance on artificial reefs than natural reef sites. Other discriminating taxa between Groups 2 and 1 included *Rypticus maculatus* and small, unidentified Scaridae (juvenile forms of five different scarids commonly encountered, all which are difficult to identify to species at juvenile and sub-adult stages). These discriminators were, on average, more abundant at the artificial reef habitats of Group 2 than the natural reef sites of Group 1. Species more prevalent on natural reef sites in the western Gulf included: *Pronotogrammus martinicensis*, *Chromis enchrysurus*, *Decodon puellaris*, *Halichoeres bathyphilus*, and *Serranus annularis*. Only *P. martinicensis* had a ratio value greater than 2.5, identifying it as a discriminating species between these two Groups. Of the 29 taxa that comprised the comparisons between Groups 1 and 2, 17 taxa (59 %) were observed from both habitat clusters.

Average dissimilarity between the eastern Gulf sites of Group 3 and the platform artificial reefs (Group 2) included 31 taxa of which 18 (approximately 58 %) were shared between the two groups (see Table 17). Fifteen taxa accounted for > 50 % of the dissimilarity, of which five (Scaridae, *Abudefduf saxatilis*, *Paranthias furcifer*, *Chromis cyanea*, and *Pomacentrus variabilis*) were identified as the best discriminators. These discriminating taxa tended to be found in higher abundance on the artificial reef platforms of Group 2. Additional discriminators identified from the platform habitats included *Rypticus maculatus*, *Holocanthus tricolor*, and *Chromis*

multilineata. Species found predominately on the eastern Gulf natural reef sites (Group 3) included *Serranus phoebe*, *Chromis insolata*, *Halichoeres bivittatus*, and *Mycteroperca interstitialis*. Because their average contributions relative to the total was small, numerous species specific to the eastern Gulf (e.g., *Hypoplectrus unicolor*, *Pomacanthus arctuatus*, and *Scarus rubripinne*) are not listed.

Although the overlap of common taxa between Groups 3 and 1 greatly increased (85 % were noted from both groups), the magnitude of the dissimilarity value between natural reef sites of the western vs. the eastern Gulf is nearly the same as the comparisons of either with the platforms (percent dissimilarity between Groups 2 and 3 = 74.7 and Groups 2 and 1 = 77.1, see Table 17). This commonality of taxa is also reflected in a depression of the ratio values, with the best discriminating species (*Holocanthus bermudensis*) having a maximal ratio value of only 1.78. Thirteen taxa accounted for > 50 % of the average dissimilarity between Groups 3 and 1, including all the discriminating species (each with a ratio value, $\delta avg_{(i)}/SD(\delta_{(i)})$, > 1.30; *Pronotogrammus martinicensis*, *Paranthias furcifer*, *H. bermudensis*, *Serranus phoebe*, and *Chaetodon ocellatus*). *Pronotogrammus martinicensis* and *P. furcifer* were more abundant in the western Gulf, while *H. bermudensis*, *S. phoebe*, and *C. ocellatus* were consistently encountered at higher abundance on natural reef sites in the east.

Multidimensional scaling of reef-dependent fisheries abundance reinforced the general west-east separation of the reef-dependent communities identified from the cluster analysis (Fig. 44). MDS ordination in three dimensions resulted in a minimum

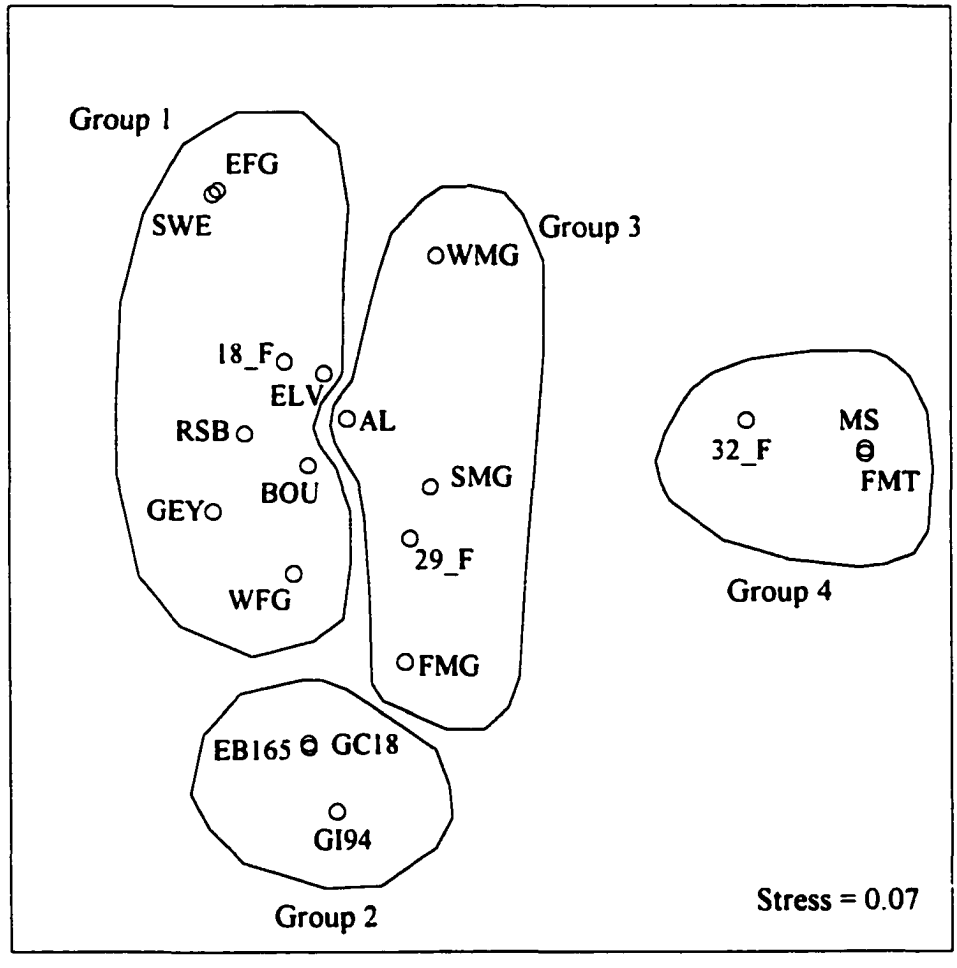


Figure 44. MDS of Bray-Curtis similarities of the 19 reef-dependent communities (2-D configuration) with superimposed Group clusters from complete linkage clustering. See Appendix C for corresponding station names.

stress of 0.05 for each of the 10 iterations, and the resulting two-dimensional MDS converged to a minimum stress of 0.07 for 8 of the 10 iterations. The difference in global minimums between the three-dimension and two-dimension solutions suggests that a two-dimension map adequately portrays the relationships among sites.

Graphical representations of the physical characteristics of the 19 habitats superimposed onto the MDS ordination is shown in Fig. 45. Western Gulf sites of Group 1 tended to be deep-water reefs with high vertical relief (as measured by the rugosity of the benthic habitat type). Only Geyer Bank, GEY (< 30 m depth) and 18-Fathom Reef (low vertical relief) differed substantially from this pattern. The eastern Gulf sites of Group 3 revealed an inverse relationship between water depth and vertical relief. The high relief sites (29_F, FMG, and SMG) were all relatively shallow water reefs, while the deeper reef sites (AL and WMG) all had low vertical relief. The platform artificial reefs of Group 2 had very low vertical relief (low rugosity of the fouling community growing on the structure) and shallow habitat depth (the majority of the reef-dependent species were found in the first 20 m of the water column).

Discussion

Based on their reef-dependent fish communities, the platform artificial reef sites (Group 2) were "biologically" more similar to the eastern Gulf natural reef sites (Group 3) than they were to the geographically closer western Gulf reef sites (Group 1). This is in contrast to the proposed larval transport routes (see Chapter 2, Results), where in terms of the direction, reef dependent supply tended to reflect larval transport coming

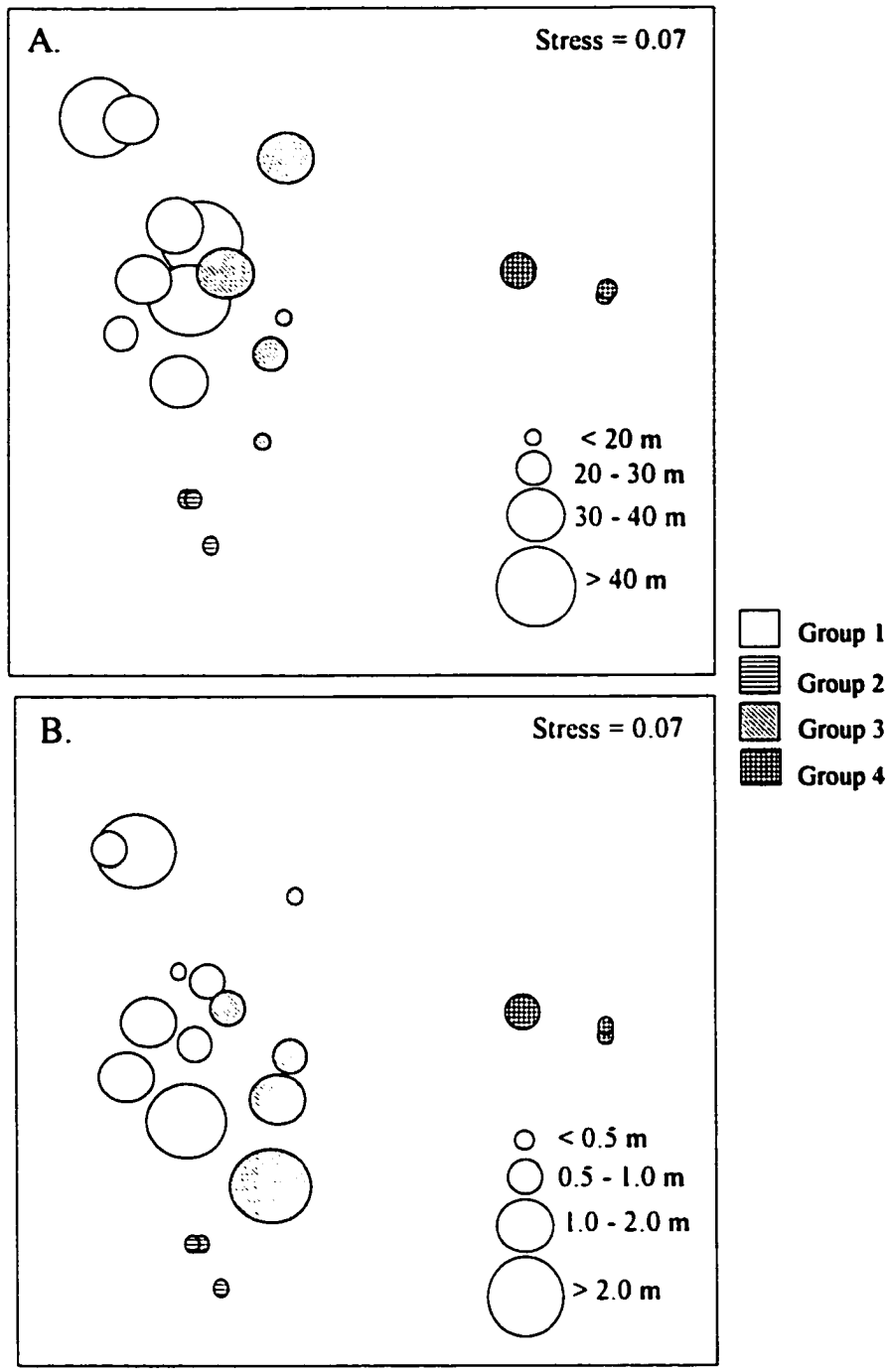


Figure 45. MDS of Bray-Curtis similarities of the 19 reef-dependent communities (2-D configuration) with superimposed linear scale circles of increasing size corresponding to A) increasing water depth, and B) increasing mean vertical relief of the reef habitat. Group shading patterns corresponds to original group designations from the complete linkage clustering.

almost exclusively from the western side of the Gulf (west of 90° W longitude). Additionally, based on the general seasonal circulation patterns identified in Chapter 2, longer larval transport durations (upwards of the one to two month envelopes presented by Roberts 1997) would have still shown little recruitment coming from the eastern side of the Gulf. Satellite altimeter derived transport envelopes showed that the vast majority of potential source locations for the platform artificial reef sites studied were other, upstream platforms. This source-sink connection is reinforced by the high degree of similarity of taxa seen with the cluster analysis, with the shelf-break platforms (EB165 and GC18) clustering highest on the dendrogram despite their physical separation of 100's of kilometers. The shelf-break platforms were then, in turn, more similar in overall reef-fish community to the mid-shelf platform than to any of the other natural reef sites.

Examining the fish community differences between the platform habitats and the western Gulf sites (dissimilarity ratio values between Groups 2 & 1) better elucidates reasons why the platforms clustered more closely with the eastern Gulf locations. Taxa with the highest ratio values (i.e., best discriminators: *Pomacentrus partitus*, *P. variabilis*, *Abudefduf saxatilis*, *Rypticus maculatus*, *Thallasoma bifasciatum*, and Scaridae) were all shallow-water forms that were found at high abundance levels on the platform habitats (although finding greater numbers of reef-dependent species on artificial reefs relative to natural reefs is not uncommon; see Bohnsack and Sutherland 1985 for review). Shallow-water forms also noted from the eastern Gulf included *P. partitus*, *P. luecostictus*, *T. bifasciatum*, Scaridae, and *Acanthurus coeruleus* (Table

17). The preponderance of these shallow-water inhabitants that are able to utilize the upper part of the water column around the platform structures enable these artificial reefs to take on a "biological character" more like the eastern Gulf, despite the majority of the larval supply opportunities coming from the west. This does not imply that these shallow-water reef fishes are not found in the western Gulf, only that they were consistently found at higher abundance levels on the platform habitats. Permanent populations of the shallow-water *A. saxatilis* have been established throughout the western Gulf on many offshore platforms (Dennis and Bright 1988), with this species occupying the uppermost reaches of the water column around the structure.

Given the extensive geographic range of platform structures in the northern Gulf, larval transport routes now encompass a far greater number of potential sink areas. Successful recruitment to the variety of niches present at these sinks, coupled with the stable environmental factors found in the upper and mid-water column, can lead to a rapid multiplication of source populations within a dominant current regime, thereby leading to a high degree of interconnectivity in the transport envelopes. From the perspective of the reef fish that have the appropriate early life history strategies that enable them to utilize these artificial reefs, the whole of the continental shelf in the northern Gulf has become effectively a large, highly interconnected, platform artificial/natural reef complex.

Understanding the extent to which artificial reefs either attract species or increase fish biomass is essential for sensible fishery management, especially if outdated platform habitats are to be utilized beyond their "de-facto" status of artificial reefs

(Wilson et al. 1987). Federal regulations currently require the complete removal of decommissioned platforms or allows for their conversion to completely submerged artificial reefs (Ditton and Falk 1981; Reggio 1996). An estimated 100 platforms per year are scheduled for decommission and/or removal (Bull and Kendall 1994). Shipping/navigation requirements necessitate that the tops of platform artificial reefs be positioned below -24 m, although proponents of artificial reef programs point out that these structures would be "ecologically" more beneficial if allowed to extend into the upper, sunlit zones (Anonymous, 1999). Based on the functional role of platform artificial reefs identified in this study, allowing the tops of the platforms to extend above -24 m would be highly beneficial to some reef-dependent species (e.g., Pomacentridae, Labridae, and Acanthuridae), yet potentially unnecessary for others (Serranidae, Pomacanthidae, and Chaetodontidae).

CONCLUSIONS

While ichthyoplankton sampling targeted larvae found only in the surface waters, the family-level taxonomic richness from the four study platforms was similar in magnitude to more comprehensive, depth-integrated surveys from the Gulf. When viewed collectively as functional groups, more reef-dependent larvae were collected in the spring and reef-associated were more prevalent during the summer, although some individual families of both functional groups also showed abundance increases in the fall. More larvae of both functional groups were collected from the deeper, shelf-break platforms.

No differences in the density of reef-dependent larvae were found among the four platforms, and no clear diurnal relationship was identified for this functional group. Significant differences in the density of reef-associated larvae were found among the four sampling locations, with the easternmost shelf-break station (GC18) receiving higher numbers of individuals than the near-shore location (ST54). On the shelf-break platforms, reef-associated larvae were more numerous in the surface waters during the early morning, whereas on the mid-shelf and near-shore platforms, greater numbers of individuals were collected at dusk.

Based on the small larvae of Serranidae, Pomacentridae, Carangidae, Lutjanidae, and Gobiidae that were collected, the larval supply of reef fishes to oil and gas platforms is indicative of local spawning. Most of the conspicuous members of the reef fish communities that were found at each platform (e.g., Scaridae, Acanthuridae,

Labridae, and Pomacanthidae) were either absent, or rarely encountered in the plankton.

Little agreement in catch composition was found between surface nets and light traps. Light traps collected fewer families, and far fewer individuals than the surface nets. Surface current speed, sweeping the larvae past the illumination chamber of the light trap, competition from the structure itself for the "attention" of photopositive fish taxa, and the choice of the light source (i.e., a directional underwater dive light) are three explanations given for the low catch rates seen with this light aggregating gear. Lighted plankton nets proved to be a more efficient light aggregation device for sampling around platform structures. Although phototaxic behavioral responses for some taxa were noted, the reef-dependent and reef-associated target taxa were not collected in statistically different numbers with this gear vs. the unlighted net.

A representative reef-dependent family (Serranidae) was used to determine the spatial area of potential spawning locations. Larval durations in the plankton, measured as days from fertilization to capture at the platform locations, averaged 14.5 days for the thirteen identifiable species/species complexes. Seasonal spawning envelopes derived from satellite altimeter measurements of sea surface height showed that for larvae in the upper water column, supply to platform habitats was primarily coming from the western portions of the Gulf. Numerically, other oil and gas platforms within these potential spawning envelopes were the most like candidates for supplying reef fish larvae to each study platform. Large scale features identified as impacting the mid-shelf and shelf-break platforms, and ultimately bring reef fish larvae in contact with

available habitats, included cold-core rings over the continental shelf as well as warm-core eddies beyond the margin of the shelf. At no time during the study did the Loop Current directly impact any of the study platforms.

Juvenile and adult reef fish populations on numerous natural reefs and submerged banks in the eastern and western Gulf wwer compared to the reef fish populations on the mid-shelf and shelf-break platforms. The platforms had a reef ichthyofaunal community more like those on the natural reefs sites found in the eastern Gulf, which were characterized as shallower-water reef communities. This is in contrast to proposed larval supply routes defined by the seasonal transport envelopes, which showed most larval supply was coming exclusively from the western side of the Gulf. Exploitable characteristics of the additional habitat afforded by platform artificial reef structures (shallow water habitat located primarily in areas devoid of natural reefs) has allowed the additional living space created by these habitats to become a highly interconnected artificial reef complex in the northern Gulf of Mexico.

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APPENDICES.

A. Experimantal design and expected mean squares.

Expected mean squares (EMS) and proper numerator and denominator for each *F* test within the nested-factorial analysis of variance of reef fish recruitment to petroleum platforms. Key to Source columns; F = fixed effect; R = random effect; σ^2; expected variance for random effects, (no sum to zero constraint); ϕ^2; expected variance for fixed effects, (sum to zero constraint). See text for explanation of Pseudo *F* test. EMS table formats follows Hicks (1993).

Model Effect	Source	4 R i	4 F j	3 R k	2 F l	3 R m	EMS	Proper *F* Test
Platform	P_i	1	4	3	2	3	$\sigma^2_\varepsilon + 6\sigma^2_{PD} + 72\sigma^2_P$	$P_i / PD_{ik(j)}$
Season	S_j	4	0	3	2	3	$\sigma^2_\varepsilon + 6\sigma^2_{PD} + 24\sigma^2_D + 18\sigma^2_{PS} + 72\phi^2_S$	Pseudo *F*
Platform × Season	PS_{ij}	1	0	3	2	3	$\sigma^2_\varepsilon + 6\sigma^2_{PD} + 18\sigma^2_{PS}$	$PS_{ij} / PD_{ik(j)}$
Day(Season)	$D_{k(j)}$	4	1	1	2	3	$\sigma^2_\varepsilon + 6\sigma^2_{PD} + 24\sigma^2_D$	$D_{k(j)} / PD_{ik(j)}$
Platform × Day(Season)	$PD_{ik(j)}$	1	1	1	2	3	$\sigma^2_\varepsilon + 6\sigma^2_{PD}$	$PD_{ik(j)} / \varepsilon$
Time(Day(Season))	$T_{l(k(j))}$	4	1	1	0	3	$\sigma^2_\varepsilon + 3\sigma^2_{PT} + 12\phi^2_T$	$T_{l(k(j))} / PT_{il(k(j))}$
Platform × Time (Day(Season))	$PT_{il(k(j))}$	1	1	1	0	3	$\sigma^2_\varepsilon + 3\sigma^2_{PT}$	$PT_{il(k(j))} / \varepsilon$
Error	$\varepsilon_{m(ijkl)}$	1	1	1	1	1	σ^2_ε	

B. Power determinations of main effect tests in each ANOVA model.

B.1. Power calculations for total ichthyoplankton density minus Clupeiformes, for significant main effects in the Model I ANOVA. Type III Sums of Squares. CI = 95 % confidence interval. LSN = Least significant number of samples to detect a significant difference.

Type I Error Rate	Sample Size	Root Mean Square Error	Effect Size	Power of Test	CI: Lower Limit	CI: Upper Limit	Least Significant Number	Power when N=LSN
Main Effect : Time								
0.05	55	0.24	0.209	0.999	0.790	1.000	22	0.694
Main Effect : Season								
0.05	55	0.24	0.216	0.999	0.838	1.000	21	0.640

B.2. Power calculations for total density of reef-dependent taxa at GC18 during 1994 and 1995, for main effects in the Model I ANOVA. Type III Sums of Squares. CI = 95% confidence interval. LSN = Least significant number.

Type I Error Rate	Sample Size	Root Mean Square Error	Effect Size	Power of Test	CI: Lower Limit	CI: Upper Limit	Least Significant Number	Power when N=LSN
Main Effect : Time								
0.05	55	0.24	0.109	0.911	0.112	0.999	33	0.639
Main Effect : Season								
0.05	55	0.24	0.070	0.527	0.050	0.996	68	0.639

B.3. Power calculations for total density of reef-associated taxa at GC18 during 1994 and 1995, for main effects in the Model I ANOVA. Type III Sums of Squares. CI = 95% confidence interval. LSN = Least significant number.

Type I Error Rate	Sample Size	Root Mean Square Error	Effect Size	Power of Test	CI: Lower Limit	CI: Upper Limit	Least Significant Number	Power When N=LSN
Main Effect : Time								
0.05	55	0.35	0.101	0.370	0.050	0.988	99	0.645
Main Effect : Season								
0.05	55	0.35	0.417	0.100	0.998	1.000	20	0.774

B.4.a. Significant main effect power calculations for total density comparisons among platforms during the summer lighted plankton net collections during 1996 and 1997. Type III Sums of Squares. CI = 95 % confidence interval. LSN = Least significant number.

Type I Error Rate	Sample Size	Root Mean Square Error	Effect Size	Power of Test	CI: Lower Limit	CI: Upper Limit	Least Significant Number	Power When N=LSN
Main Effect : Platform								
0.05	41	0.32	0.261	0.997	0.600	1.000	14	0.601

B.4.b. Significant main effect power calculations for seasonal total density comparisons with the lighted plankton net collections at GI94 in 1996 and 1997. Type III Sums of Squares. CI = 95 % confidence interval. LSN = Least significant number.

Type I Error Rate	Sample Size	Root Mean Square Error	Effect Size	Power of Test	CI: Lower Limit	CI: Upper Limit	Least Significant Number	Power When N=LSN
Main Effect : Season								
0.05	51	0.27	0.239	0.999	0.898	1.000	13	0.620

B.5. Main effect power calculations for seasonal total density comparisons of reef-dependent taxa with the lighted plankton net collections at GI94 in 1996 and 1997. Type III Sums of Squares. CI = 95 % confidence interval. LSN = Least significant number.

Type I Error Rate	Sample Size	Root Mean Square Error	Effect Size	Power of Test	CI: Lower Limit	CI: Upper Limit	Least Significant Number	Power when N=LSN
Main Effect : Season								
0.05	41	0.21	0.079	0.520	0.050	0.992	46	0.588
Main Effect : Light								
0.05	41	0.21	0.047	0.284	0.050	0.916	79	0.508

B.6. Main effect power calculations for total density comparisons of reef-associated among platforms during summer lighted plankton net collections during 1996 and 1997. Type III Sums of Squares. CI = 95 % Confidence interval. LSN = Least significant number

Type I Error Rate	Sample Size	Root Mean Square Error	Effect Size	Power of Test	CI: Lower Limit	CI: Upper Limit	Least Significant Number	Power when N=LSN
Main Effect : Platform								
0.05	46	0.21	0.091	0.631	0.051	0.996	38	0.593
Main Effect : Light								
0.05	46	0.21	0.019	0.097	0.050	0.588	1,278	0.503

B.7. Main effect power calculations for seasonal total density comparisons of reef-associated taxa collected with the lighted plankton net collections at GI94 in 1996 and 1997. Type III Sums of Squares. CI = 95 % confidence interval. LSN = Least significant number.

Type I Error Rate	Sample Size	Root Mean Square Error	Effect Size	Power of Test	CI: Lower Limit	CI: Upper Limit	Least Significant Number	Power When N=LSN
Main Effect : Platform								
0.05	45	0.32	0.1780	0.9362	0.1992	0.9999	24	0.6058
Main Effect : Light								
0.05	45	0.21	0.0141	0.0607	0.0500	0.6064	1,982	0.5003

C. Physical characteristics of 16 natural reef sites from the northern Gulf of Mexico.

Physical characteristics of the 16 natural reef sites from the northern Gulf of Mexico sampled with the fish trap/video deployments. Data provided by the SEAMAP Program, National Marine Fisheries Service, Pascagoula, Mississippi. Station abbreviations used in cluster analysis and multidimensional scaling analysis in text. *N* video samples = numbers of samples (in hours) of video tape from each station. Water depth (standard deviation in parenthesis) in meters, recorded from ships log; Maximum Vertical Relief and Mean Vertical Relief (in meters); and Dominant Relief Type estimated directly from tapes by readers.

Station	Abbreviation	*N* Video Samples	Latitude-Longitude	Water Depth	Max. Relief	Mean Relief	Dominant Relief Type
32 Fathom Reef	32_F	4	28°03.8'N 94°31.3'W	28.0 (0.8)	0.75	0.1	Sand / Silt, Low Dunes, Few Live Bottom Structures
29 Fathom Reef	29_F	2	27°55.0'N 93°27.0'W	29.0 (4.2)	1.5	0.5	Hard Bottom Outcrops, Many Octocorals and Anthipatharians
18 Fathom Reef	18_F	2	27°58.0'N 92°36.0'W	38.7 (4.6)	1.50	0.5	Low Relief, Sandy / Silt Bottom, Scattered Macroalgae Patches Antipatharians
West Flower Garden Bank	WFG	12	27°52.5'N 93°49.0'W	32.2 (13.1)	2.5	0.8	Hard Bottom, Live Coral Boulders, Sand, Macroalgae, Octocorals

Appendix C. (cont.)

Station	Abbreviation	*N* Video Samples	Latitude-Longitude	Water Depth	Max. Relief	Mean Relief	Dominant Relief Type
East Flower Garden Bank	EFG	17	27°54.5'N 93°36.0'W	34.8 (9.6)	4.0	1.2	Hard Bottom, Live Coral Boulders Coral Rubble, Macroalgae
Geyer Bank	GEY	2	27°51.6'N 93°04.0'W	29.5 (4.9)	1.5	0.6	Rock / Coral-Algal Substrate, Sponges, Soft Coral, Little Sand
Elvers Bank	ELV	5	27°49.0'N 92°53.5'W	55.0 (5.7)	1.0	0.2	Rocky Outcrops with Sand Patches, much Macroalgae and some Antipatharians
Rezak – Sidner	RSB	4	27°57.0'N 92°23.0'W	39.4 (9.2)	1.5	0.3	Low Rolling Hills with Rocky Coral Mounds, Alcyonarians, Sand and Algal Patches
Sweet Bank	SWE	2	27°51.0'N 91°49.0'W	59.5 (5.8)	1.0	0.2	Low Rock / Rubble, Solitary Antipatharians in Sand Patches, Scattered Coral Heads
Bouma Bank	BOU	4	27°58.9'N 92°23.6'W	43.3 (6.1)	0.7	0.2	Sand/Silt with Sparse Rocky Pinnacles, Few Soft Corals and Sea Whips
Mississippi Shelf	MS	2	29°41.0'N 88°06.6'W	19.8 (1.8)	0.1	0.1	Low Sandy Bottom, Little Relief Vertical Relief

Appendix C. (cont.)

Station	Abbreviation	*N* Video Samples	Latitude-Longitude	Water Depth	Max. Relief	Mean Relief	Dominant Relief Type
Alabama Shelf	AL	4	29°55.0'N 87°10.0'W	32.0 (-*)	1.0	0.4	Small, Isolated Patch Reefs with Rubble Areas, Sponges and Antipatharians
West Florida Middle Ground	WMG	6	28°55.0'N 85°17.5'W	37.7 (2.7)	0.5	0.1	Low Relief Coarse Sandy Bottom, Few Soft Corals Among Scattered Rock Mounds
Florida Middle Ground	FMG	34	28°27.0'N 84°19.5'W	17.7 (1.8)	2.5	0.6	Rocky Mound Bottom, Coral Heads and Sponges, Macroalgae and Carbonate Sand
South Middle Ground	SMG	11	28°41.6'N 84°23.9'W	15.9 (2.6)	1.0	0.2	Rubble / Sand Bottom, Low Form Algal Mats, Scattered Small Coral Patch Reefs
Fort Myers Triangle	FMT	7	26°34.3'N 82°32.3'W	9.9 (0.9)	0.1	0.1	Hard Sand/ Silt Bottom, Little Vertical Relief

VITA

James M. Tolan was born in Corpus Christi, Texas on September 1, 1964. His parents are the late James C. Tolan and Mary Jo Tolan, of Artesia, New Mexico. He received his elementary education in San Diego, California, Pensacola, Florida, and Dededo, Guam. He received his secondary education at Flour Bluff High School, Corpus Christi, Texas. He attended Del Mar Community College in Corpus Christi, Texas 1987-1989 majoring in biology. He attended Corpus Christi State University / Texas A&M-Corpus Christi 1989-1994 majoring in biology and received a bachelor of science with Honors in 1992. He was awarded a master of science in marine science in 1994.

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DOCTORAL EXAMINATION AND DISSERTATION REPORT

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Major Field: Oceanography and Coastal Sciences

Title of Dissertation: Patterns of Reef-Fish Larval Supply to Petroleum Platforms in the Northern Gulf of Mexico

Approved:

Major Professor and Chairman

Dean of the Graduate School

EXAMINING COMMITTEE:

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October 11, 2000